

Conservation Status, Ecology, and Distribution of Desert Tortoises in Mexico

The Mexico Tortoise Project, 2001-2013

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Executive Summary

We surveyed 43 localities in Sonora and Sinaloa, Mexico during 2005-2013 to collect information on the status, ecology, and genetics of desert tortoises (*Gopherus morafkai*). We measured and photographed animals we captured, in addition to collecting samples for genetic and health status studies. We also obtained and digitally georeferenced available records of the species' distribution from museum databases, published literature, and observations from individuals who supplied us with photo documentation. The distribution of this species in Mexico is composed of two divergent genetic groups represented by an ancient mitochondrial DNA (mtDNA) haplogroup divergence that is concordant geographically with divergence of nuclear genes. There is a desert type in subtropical Sonoran Desertscrub and marginal, relatively less mesic thornscrub (the "Sonoran" tortoise, *G. morafkai sensu stricto*) and a Sinaloan type in tropical deciduous forest (TDF) and tropical thornscrub (the "Sinaloan" tortoise, which is likely to be recognized taxonomically in the near future but currently remains within *G. morafkai*). However, the distribution of desert tortoises in Mexico is continuous within desertscrub, thornscrub, and TDF in suitable habitat with rock or other hard shelters. There are genetically intermediate areas in parts of the thornscrub, and the speciation process between Sonoran and Sinaloan desert tortoises is more spatially complex than the recently formalized species difference between Sonoran and Mojave (*G. agassizii*) desert tortoises. About half of the range of *G. morafkai* in Mexico comprises the undescribed Sinaloan form and a contact zone in which mtDNA haplotypes and nuclear genes are both present in populations and some individuals.

The distribution of the Sonoran tortoise includes most, if not all rocky environments, and surrounding bajadas often to ≥ 3.5 km from the slopes, from the highly arid Pinacate Biosphere Reserve and Central Gulf Coast subdivision of the Sonoran Desert, east through the Plains of Sonora subdivision and into thornscrub in the foothills and mountain bases below the Sierra Madre Occidental. Its known elevational range is 5–1210 m in Mexico. We have not found it above the desert and thornscrub in semi-desert grasslands or higher elevation environments. The Sinaloan tortoise is abundant in the region of Alamos in rich TDF, which it follows north along the base of the Sierra Madre into east-central Sonora. A recent published record demonstrates that it follows a like corridor also into southwestern Chihuahua. We also found Sinaloan tortoises in thornscrub in northern Sinaloa, where it extends south to at least Topolobampo, and in central-southern Sonora.

We found very little evidence of mortality in Sinaloan tortoise populations in TDF in either Sonora or Sinaloa, although this may reflect decomposition of carcasses after predation. In contrast, in thornscrub we found carcasses at several localities, in both states, including in a high proportion in samples from thornscrub in Sonora. We found some evidence of elevated mortality in the northwestern deserts in Sonora in 2012, and previously (2001-02) observed mass mortality and population reduction at study sites in central coastal Sonora. Mortality patterns showed an association with drought and the heat of low-elevation environments.

We discuss several threats to desert tortoises in Mexico, among which climate change is the most serious. Based on projections of down-scaled climate models for southwestern North America, the region will become hotter and drier through the coming decades of this century, and drought frequency

and severity are projected to increase. *G. morafkai* may face serious climate-driven declines continuing a trend of episodic, drought-related mortality episodes, which we have documented in detail for localities through much of the desertscrub and thornscrub region occupied by genetically Sonoran *G. morafkai*. More detailed modeling is needed to specify this threat more precisely, but, unless anthropogenic climate change is stopped, continuing decline of abundance of *G. morafkai* is highly likely.

A second major threat to *G. morafkai* is conversion of native desertscrub and thornscrub to induced buffelgrass pasture in Mexico and the rapid and continuing self-spread of buffelgrass into native vegetation occupied by *G. morafkai*. As with climate change, this threat is more pronounced in desertscrub and thornscrub than in TDF. Buffelgrass spreads fire into non-fire adapted scrub communities, eliminating shade trees and killing tortoises; it also appears to outcompete preferred plants comprising the diet of *G. morafkai*, and may thereby degrade the body condition of tortoises, exposing them to further risk associated with climate warming and drying as well as other threats that may arise, such as disease. In TDF, buffelgrass severely degrades the operative thermal environment for desert tortoises, but this grass does not take over the native vegetation, and is quickly replaced by second growth of native species if these are not regularly controlled. Thus, the buffelgrass problem is more severe and less tractable from a conservation management standpoint in desertscrub and thornscrub than in TDF.

Among the several other impacts that might threaten *G. morafkai*, road mortality is the best known and most likely to increase in severity. Although *G. morafkai* is still eaten by people in Mexico, this threat has decreased greatly in recent decades. More people use tortoises as pets, by far, than eat them, which may locally deplete some populations. A greater potential threat emanating from the use of desert tortoises as pets is facilitation of disease processes, with introduction of exotic reptile diseases into wild populations of greatest concern, although only as a potential threat. We found *G. morafkai* abundant at numerous localities in Mexico, and we found it at almost all localities we sampled even though sampling was often brief. Without the threats of climate change and buffelgrass, we would have limited concerns for the future of this species in Mexico or the United States.

Chapter 1 Distribution and Conservation Status of Desert Tortoises in Northwestern Mexico

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ABSTRACT

We surveyed 43 localities in Sonora and Sinaloa, Mexico during 2005-2013 to collect information on the status, ecology, and genetics of desert tortoises (*Gopherus morafkai*). We measured and photographed animals we captured, in addition to collecting samples for genetic and health status studies. We also obtained and digitally georeferenced available records of the species' distribution from museum databases, published literature, and observations from individuals who supplied us with photo documentation. The distribution of this species in Mexico is composed of two genetic lineages where ancient mitochondrial DNA (mtDNA) haplogroup divergence is concordant geographically with strong population genetics observed in nuclear genes. There is a desert type in subtropical Sonoran Desertscrub and marginal, relatively less mesic thornscrub (the "Sonoran" tortoise, *G. morafkai* sensu stricto) and a Sinaloan type in tropical deciduous forest (TDF) and tropical thornscrub (the "Sinaloan" tortoise, which is likely to be recognized taxonomically in the near future but currently remains within *G. morafkai*). However, the distribution of desert tortoises in Mexico is continuous within desertscrub, thornscrub, and TDF in habitat with rock or other hard shelters. There are genetically intermediate areas in parts of the thornscrub, and the speciation process between Sonoran and Sinaloan desert tortoises is more spatially complex than the recently formalized species difference between Sonoran and Mojave (*G. agassizii*) desert tortoises. About half of the range of *G. morafkai* in Mexico comprises the undescribed Sinaloan form and a contact zone in which admixture is observed in populations. The distribution of the Sonoran tortoise includes most, if not all rocky environments, and surrounding bajadas often to ≥ 3.5 km from the slopes, from the highly arid Pinacate Biosphere Reserve and Central Gulf Coast subdivision of the Sonoran Desert, east through the Plains of Sonora subdivision and into thornscrub in the foothills and mountain bases below the Sierra Madre Occidental. Its known elevational range is 5–1210 m in Mexico; we have not found it above the desert and thornscrub in semi-desert grasslands or higher elevation environments. The Sinaloan tortoise is abundant in the region of Alamos in rich TDF, which it follows north along the base of the Sierra Madre into east-central Sonora. A recent published record demonstrates that it follows a like corridor also into southwestern Chihuahua. We also found Sinaloan tortoises in thornscrub in northern Sinaloa, where it extends south to at least Topolobampo, and in central-southern Sonora. We found very little evidence of mortality in Sinaloan tortoise populations in TDF in either Sonora or Sinaloa, although this may reflect decomposition of carcasses after predation. In contrast, in thornscrub we found carcasses at several localities, in both

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1.1 INTRODUCTION

Morafka's desert tortoise (or the Sonoran Desert tortoise, *G. morafkai*) is being considered for listing under the U.S. Endangered Species Act (USFWS 2010) based on a suite of threats and evidence for recent population declines at some sites in Arizona. Approximately 40% of the species distribution occurs in Mexico, where there is little available information on species status or trends. This chapter describes the distribution and discusses known and potential threats to the species in Mexico. It draws on data and experience from the Mexico Tortoise Project, a collaboration of multiple researchers and agencies from the United States, Mexico, and Canada during 2001-2013, which are presented here and in following chapters that treat specific aspects of the problem for which we obtained key, though in some cases preliminary results and in which we draw on data from Arizona for supporting interpretation.

Threats to biodiversity in northwestern Mexico, many of which affect desert tortoises, are reviewed by Stoleson et al. (2005), and range-wide threats to *G. morafkai* have been summarized elsewhere (USFWS 2010; Western Watersheds Project and WildEarth Guardians, 2008). Here we present evaluations based

on what is known about specific threats to desert tortoises in Mexico and our observations elsewhere relevant to this specific evaluation.

1.2 METHODS

Sampling was initiated with fieldwork led by Mercy Vaughn in the Comcáac lands (Seri Coast) of Sonora near Tiburon Island in 2001-2002. In 2005, we began a wider study in collaboration with Cristina Melendez of CEDES (Comisión de Ecología y Desarrollo Sustentable del Estado de Sonora), the state conservation authority of Sonora, to investigate various aspects of tortoise ecology in Mexico. We initiated fieldwork to collect samples for genetic analysis by Taylor Edwards and for health studies led by Dr. Mary Brown and Dr. Kristin Berry, and a telemetry-focused study on movements and coversite, microhabitat and habitat use was initiated in Alamos, Sonora, by Dr. Alice Karl. Dr. Karl further initiated a morphometrics study, with assistance from Dr. Philip Rosen, based on the initial observations in 2005. During 2005-2006 and 2008-2011, teams of volunteers were led by us in late summer and fall fieldwork. Continuous telemetry study was done 2005-2013 in Alamos. During summer and fall of 2012 and 2013, Dr. Rosen led transect-based fieldwork and initiated thermal ecology studies of desert tortoises in Sonora, working with a group of students and researchers from Mexico City and California. In fall, 2014, this work was expanded by Dr. Rafael Lara-Resendiz in Alamos and central Sonora. Sampling locations are shown in Fig. 1.

Fieldwork in 2001-2002 was focused on 0.5–1 km² plot studies and involvement of Comcáac personnel in the research, and is detailed in Chapter 3. During 2005-2011, fieldwork consisted of volunteer teams of experienced tortoise field biologists searching for and processing tortoises at localities selected for safety and likely tortoise abundance. Results from this work are included here and in Chapters 2 and 7 and in Edwards et al. (2012, and *submitted manuscript*) and Berry et al. (*in press*). During 2012-2013, fieldwork was focused on formal transects to measure observation rates of tortoises and other animals detected during the surveys at previously selected and new localities in the range of biotic communities occupied by tortoises in Sonora (see Chapter 7). Results of this work are also summarized here and detailed in Chapters 2 and 7. In 2012 and 2013 we initiated a study of the thermal ecology in relation to climate change and habitat transformation of *G. morafkai* in Mexico using operative temperature models, which is discussed here and in Chapter 6.

Interviews were done whenever possible with knowledgeable people participating in and interacting with participants in the fieldwork. We asked about where tortoises were seen, in what habitats they were found, their abundance and trends, their habits and threats they faced, and whether they were being used in various ways by people.

We reviewed published literature and reports pertaining to studies of desert tortoises (Reyes and Bury 1982; Treviño et al 1994; Bury et al. 2002; Fritts and Jennings 1994; Loomis and Geest 1964; Patterson 1982; Germano et al. 1994; Vargas 1994; Auffenberg 1969; Bogert and Oliver 1945; Bury et al. 1978) and distributional records in Mexico (Smith and Smith 1979; Lemos-Espinal and Smith 2007; Smith et al. 2004). Distributional records were obtained from the following institutions, either directly or through the HerpNet data portal: by acronym (see Leviton et al. 1985), the museums are AMNH, ANSP, ASU, CAS, CM, CNAR, FLMNH, FMNH, FSM, IPN, KU, LACM, LSU, MCZ, MSB, MVZ, SDNHM, SMNS, TNHC, UAZ,

UIMNH, USNM, and UTEP. We were provided detailed data from the MABA database of Sky Island Alliance, including photographs of recent tortoise records (T. Van Devender, pers. comm.), and received notes pertaining to fieldwork in Mexico by T. Fritts, N. Scott, and R. Jennings (T. Giermakowski, pers. comm., 2014). For comparison, we also reviewed the broader literature pertaining to ecology, evolution, and conservation biology of desert tortoises throughout their distribution.

Climatic data for environments occupied by desert tortoises were obtained from the National Climate Information Center (<http://www.ncdc.noaa.gov/cdr/index.html>), WorldClim Global Climate Data (<http://www.worldclim.org/>), Prism Climate Group (<http://www.prism.oregonstate.edu/>), and published literature. Detailed analyses of these data are presented in Chapters 2-5 and summarized and synthesized here.

1.3 RESULTS AND DISCUSSION

1.3.1 Distribution

The known distribution of *G. morafkai* in Mexico is shown in Fig. 2. It occurs throughout the Sonoran Desert in Sonora, at least as far west as the arid El Pinacate volcanic region in extreme northwestern Sonora. However, it is unknown, as yet, in the hyperarid, isolated, poorly sampled Sierra del Rosario in Gran Desierto west of the Pinacate. This tortoise also occurs throughout the Sinaloan Thornscrub of Sonora and northern Sinaloa, and throughout the Tropical Deciduous Forest of (TDF) Sonora and at least parts of northern Sinaloa and southwestern Chihuahua, where the southern and southeastern range limits remain incompletely known. *G. morafkai* in Mexico is not known from Semi-desert Grassland or the lower reaches of Madrean Oak Woodland, although it occurs marginally in these environments in Arizona (as indicated in Fig. 2) where these temperate environments closely contact subtropical desertscrub and dry tropical scrub with affinities to thornscrub. As in Arizona, the species is largely tied to rocky features, including both bajada arroyos with exposures of cemented alluvium or bedrock and rocky slopes of mountains, foothills, and isolated buttes and hills. Although there is no known use of flat plains, notably on the great delta floodplains of the ríos Sonora, Yaqui, Mayo, and Fuerte in coastal Sonora and Sinaloa, these were not sampled prior to their complete conversion to modern irrigation agriculture. Records from southernmost coastal Sonora suggest the species may occur, or may have occurred, in some sandy areas that are much less rocky than normally expected, although further sampling is required to distinguish this from a possibility these were released captives. Although Fig. 2 suggests two gaps within the distribution of the species in Mexico, northwest of Hermosillo in the rugged mountain masses of the Plains of Sonora and between Alamos and Rosario Tesopaco east of Ciudad Obregon in TDF. In both cases these gaps reflect an absence of sampling. We attempted to enter the region northwest of Hermosillo in both 2012 and 2013 but it was deemed unsafe. A search of museum records disclosed only two specimen records for herpetofauna in the Quiriego region east of Obregon, accounting for the gap there. Both gaps contain an abundance of suitable habitat (based on topographic maps and aerial imagery), so undoubtedly support populations of *G. morafkai* that are likely robust, based on the continuous habitat.

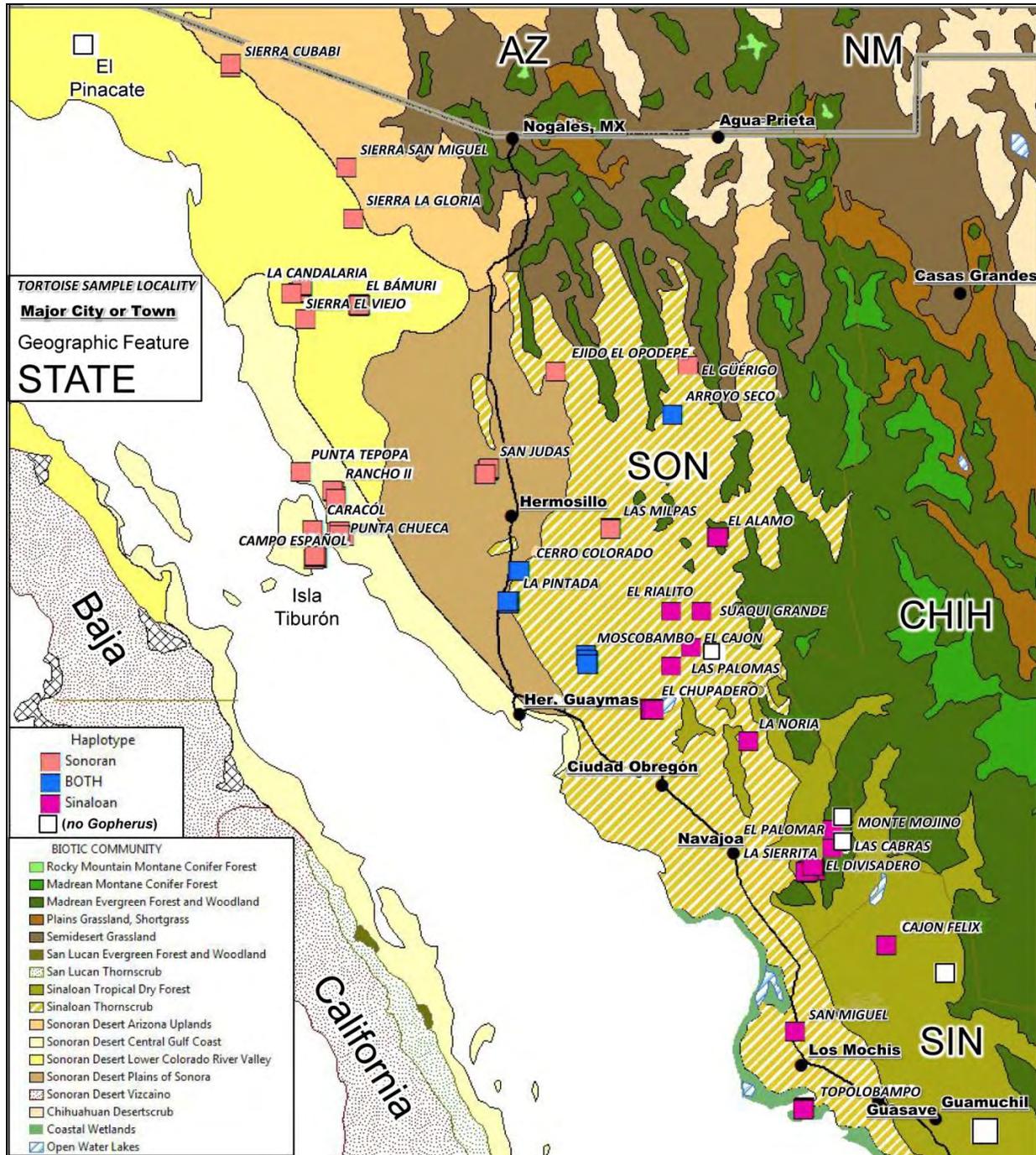


Figure 1.1. Sampling locations for tortoises in northwestern Mexico during 2005-2013, observed haplotypes, and generalized vegetation following Brown, Lowe, and Pase (1980). Source for haplotype data: Edwards et al. (2012, and submitted manuscript).

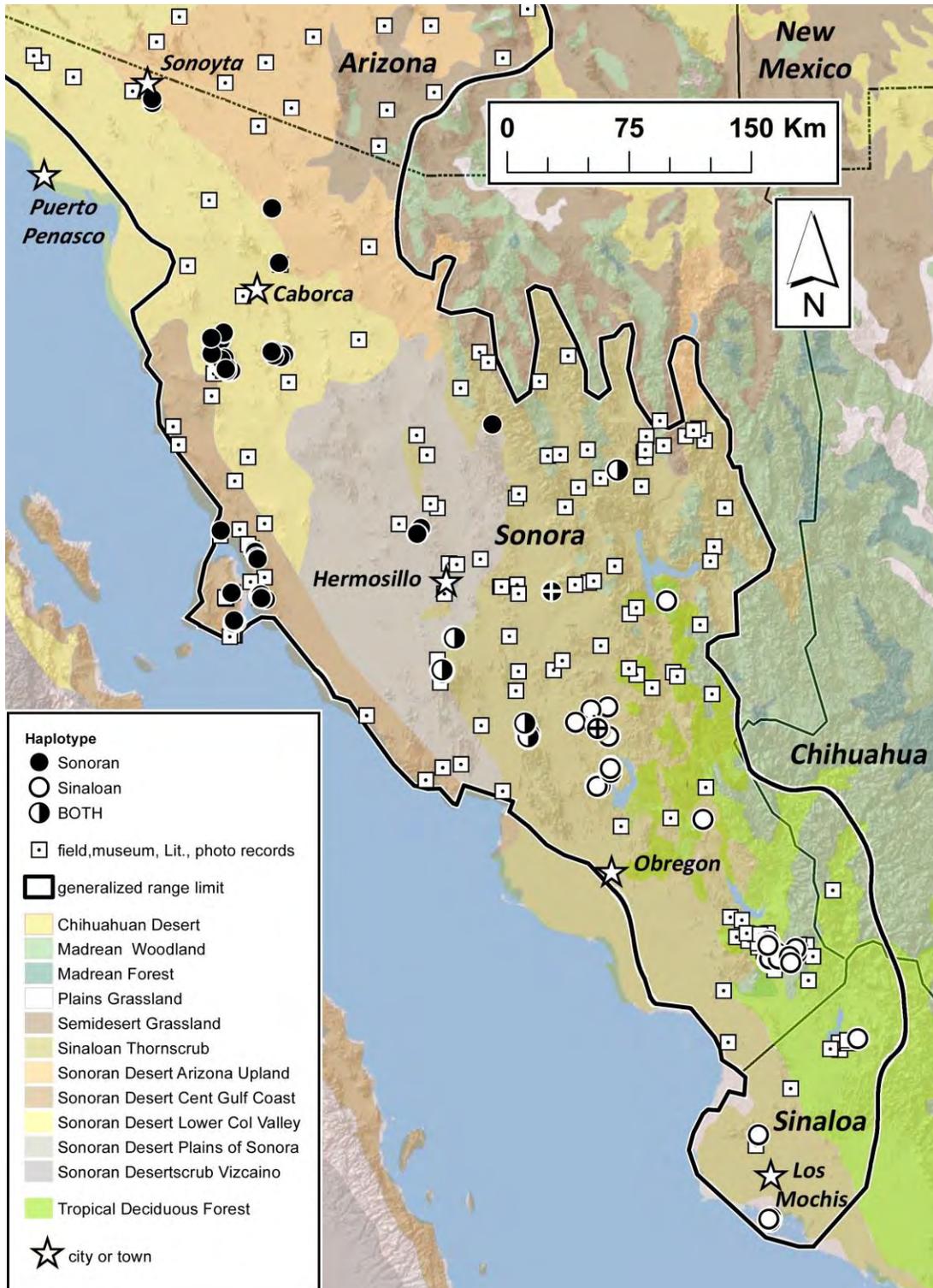


Figure 1.2. Distributional records for *G. morafkai* in Mexico. Two localities indicated by “+” had individuals with mixed Sonoran and Sinaloan nuclear genotypes (Edwards et al., *submitted*). Biomes shown are equivalent to those in Fig. 1.1, except that here we follow Martínez-Yrizar et al. (2010) regarding the distribution of tropical deciduous forest in Sonora. Underlying topography is illustrated by shading. Selected records in Arizona, USA, are included to illustrate occurrence in areas mapped as semi-desert grassland and Madrean (oak) woodland (see text).

The elevational range for all *G. morafkai* records in Mexico is 5-1210 m, with maximum ranges of 5-725 m in Sonoran Desert scrub, 29-1201 m in Sinaloan Thornscrub, and 94-843 in TDF. These elevational extremes approximately correspond to the ranges of elevations for the three biomes.

We note here that two taxa of desert tortoises occur in this distributional area in Mexico, a Sonoran Desert taxon (*G. morafkai* sensu stricto) and a Sinaloan form that is as different genetically and morphologically from *G. morafkai* (sensu stricto) as the latter is from *G. agassizii* (Edwards et al. 2012, and *submitted*; Karl et al. 2006). Pure or nearly pure populations of the Sonoran tortoise occur in the Sonoran Desert and northern part of the Sinaloan Thornscrub, while pure or nearly pure populations of the Sinaloan tortoise occur in the TDF and southern and eastern parts of the thornscrub. Populations and individuals with mixed or intermediate genetic characteristics occur in a 50-80 km wide band between these areas, as suggested by Figs. 1 and 2 and detailed by Edwards et al. (*submitted*). The distribution of Sonoran and Sinaloan lineages of *G. morafkai* at the ecotone may correspond to a “mosaic model”, which describes patchy environments where different parental lineages have a high probability of coming into contact with one another, but mating results in hybrids that are less fit ((Edwards et al., *submitted*). Thus, about half of the distribution of *G. morafkai* in Mexico is occupied by Sonoran tortoises in the strict sense. Recognition of the Sinaloan tortoise as a species or subspecies is likely in the near future.

1.3.2 Threats

1.3.2.1 Weather and Climate Change – Anthropogenic Global Warming

We have presented evidence for significant climatic and drought effects on *G. morafkai* in Mexico in Chapters 2-5 of this report. The most significant observation was a mass mortality episode discovered by Vaughn et al. (Chapter 3). In 2001-02 they found evidence of massive mortality (62.8 % dead in a sample of 78 individuals on three study plots (0.5 - 1-km²) on Isla Tiburón and adjoining coastal Sonora. This mortality was not evident on Tiburón during Reyes and Bury's (1982) study in 1978-1979, and was associated with evidence for major reduction of tortoise abundance. High mortality was again observed again when we revisited the region in 2009 and 2010. Mortality onset was correlated with the 1995-1997 onset of drought and maximum temperatures for the period of observation (Chapter 3). Although few data are available for Sonora during 2005-2014, 2009 precipitation in Hermosillo was 132 mm total (http://www.tutiempo.net/clima/Hermosillo_Son/2009/761600.htm), 54 mm below the lowest on record for 1966-2004, although comparable values were recorded during the 1950's drought and in 1965. Thus, the high mortality in 2009-2010 was associated with drought, although the weather record for 2008-2012 is limited.

Second, based on the proportion of carcasses to live tortoises in field samples, we identified a regional pattern of mortality in 2005-2013 field sampling (Chapter 2). We found evidence of significantly elevated mortality in the Tiburón region of the Central Gulf Coast subdivision of the Sonoran Desert (50% of 40 individuals found dead; $P < 0.01$ compared to other contemporaneous samples, except as follows). We also found evidence of high mortality in the central-southern Sinaloan Thornscrub of Sonora at low elevation (36.5% of 52 individuals found dead; $P < 0.01$ compared to other contemporaneous samples, except the foregoing). In the Lower Colorado River Valley (LCV) subdivision

in 2012 we discovered somewhat elevated mortality at two ranches that were associated with a 2010-2011 drought period. Geographically, *G. morafkai* mortality in Mexico during this period was associated in a best linear model with intra-biome areas of low precipitation ($P < 0.001$), low latitude ($P < 0.001$), and high temperature ($P < 0.05$), which is consistent with a general pattern of climatic stress. Tortoise population samples from regions with less arid climates, in the TDF and the more northerly thornscrub at higher, cooler elevations, had much lower observed mortality.

We also present an analysis of population trends and correlated mortality observations based on long-term data from *G. morafkai* census plots in Arizona (Chapter 5). Linear models showed that mortality observed in the form of carcasses was a highly significant predictor ($P < 0.0001$) of population change. Major population reductions ($\geq 60\%$) involving mass mortality occurred in 4 of 17 study populations and similar but possibly more gradual decline in a fifth study population during 1987-2006. Results demonstrated that calculated population declines, which were catastrophic at four sites, were associated with drought and rising regional temperatures during recent decades. Two-year running mean of precipitation, a measure of drought severity and duration, was the best linear correlate ($P < 0.05$) of mortality rates derived from sample mortality fractions, although the mortality data may not be precise enough to fix the drought durations that produced population declines. This is consistent with Zylstra et al.'s (2012) mark-recapture model demonstrating that *G. morafkai* survivorship was most strongly predicted by drought. Based on our analysis (Chapter 5), mortality fractions $\geq 17\%$ observed in formal surveys are likely to reflect reductions in abundance, and fractions in excess of 30% are likely to reflect catastrophic reductions ($\geq 60\%$) in abundance.

We summarized 18 findings from varied sources demonstrating that such high mortality fractions have been observed through much of the range of *G. morafkai* outside the TDF, and most have been clearly associated with drought episodes (7 in 1987-1991, 1 in 1995-1996, 6 in 1999-2003, and 1 ongoing through the first decade of the 21st century; Chapter 5). We summarized data from the south-central deserts of Arizona (Organ Pipe Cactus National Monument and the East Tactical Range of the Barry M. Goldwater Air Force Range) showing that tortoise mortality there was widespread there, rather than localized or isolated as has been maintained, during the 1987-1991 period (see Chapters 4 and 5). Based on a review of the global and regional climate-change literature, which projects warming, drying, and increased drought duration and severity for the North American Southwest, anthropogenic global warming appears to be the most ubiquitous, increasing, intractable, and severe threat facing *G. morafkai* in desertscrub and thornscrub. There are uncertainties in projections of precipitation change in the region, although a great majority of climate models agree and the physical principle of "warmer equals drier" makes a negative impact on *G. morafkai* of regional climate warming, for which models have consensus, likely to highly likely.

Given the weather- and climate-associated population declines we have detailed (Chapters 2-5) – which are most conspicuous as episodic, local to sub-regional, but widespread – even under best-case scenarios for further anthropogenic regional warming of about 1.5 C on top of 1 -1.5 C warming since the early-mid 1960s, continuing climate-change type mortality and abundance declines in *G. morafkai* over the next 65 years are likely inevitable. Given the extensive climatic, latitudinal, and elevational tolerance range of this species, extinction within the current distribution seems unlikely except in worst

case scenarios of anthropogenic warming of around 4.4 – 8.5°C. These worst-case model scenarios are not unreasonable brackets on the possible, however, but projections based on potential political and economic realities that are well within the realm of possibility within the current century. Extinctions are likely to occur first in the hot, arid, lower Gila Valley (Cabeza Prieta National Wildlife Refuge and Barry M. Goldwater Air Force Range), where virtually no population status studies have been conducted (see Chapter 4). We need more refined understanding of mortality and recruitment processes within desert tortoises, and at a minimum renewed ideas for active conservation management under trends of urbanization, exotic plant spread, and livestock grazing that may all interact with physiological stress entailed by climate change.

1.3.3 Collecting

Throughout the range of the desert tortoise that we explored in Mexico, everyone we spoke to was aware of tortoises. Overwhelmingly, if not universally, people had a positive or at least neutral sense about tortoises, and no one indicated that they didn't deserve protection.

1.3.3.1 Keeping as Pets and Translocation

The potential magnitude of use of tortoises as pets can be inferred from Jacobson et al.'s (1995) estimate of 200,000 *G. agassizii* in captivity in California, which is over two-thirds of a recent estimate for the wild population of the species (Allison and McCoy 2014). Informants told us in numerous instances of tortoises being kept as pets in cities, towns, and villages, and often reported captive tortoises reproducing in yards. One informant in the Hermosillo area reported releasing captive-bred tortoises to the wild, supposedly to where the parents originated, although not enough detail was provided to credit this. In Caborca, informants told us they knew of several people with pet tortoises, with large numbers of hatchlings. We found captive tortoises as pets at a ranch, and were informed that this was not common. Centro Ecologico de Sonora, Hermosillo, had over 50 tortoises that were brought in by various citizens, either as unwanted pets or after being "saved" from roads, etc. We found a tortoise at one site, La Pintada, near the main highway south of Hermosillo, with a marginal scute ring presumably used to keep it as a pet. The Las Cabras telemetry study site at Alamos was abandoned when we discovered that one or more tortoises were collected as pets. One captive was tracked about 20 km east near a small village, Sabinito Sur, with signs of captivity but walking back toward Alamos. At Sabinito Sur in 2013 we were given locality information on two pets, a long-term pet juvenile *Rhinoclemmys pulcherrima* and a small juvenile tortoise, which was presented to us for release where it came from. Two tortoises near Alamos were found painted with Mexican national colors, having apparently escaped captivity. At Sierra El Viejo, ranch managers reported that they sometimes collected tortoises from the road – which led past their ranch – and moved them up to 30 or 40 km to their ranch, where they were protected from collection by people further south who ate tortoises (see below).

Our experience suggests that the primary human interactions with desert tortoises in Mexico involve seeing them in the wild, keeping them as pets, and protecting them from harm. Tortoise translocation is undoubtedly common in Sonora, and captive tortoises, some which will be released or escape to the wild, were the only confirmed cases of *Mycoplasma* disease we found (see below; Berry et al., *in press*). Johnson et al. (2006) estimated that 4,400 captive *G. agassizii* may escape each year, some of which

may interact with natural populations. Genetic and epidemiological effects of translocation (Edwards and Berry 2013) could become a significant, growing threat to desert tortoise population in Mexico, particularly if, as may be predictable, other species of *Gopherus* and other exotic tortoises become part of the pet trade.

1.3.3.2 Tortoises as Human Food

It was not always thus: Fritts and Jennings (1994) reported frequently finding tortoise carcasses around human residences, collected a number of examples, and were given live tortoises as specimens, some of which were destined to be used as food (T. Fritts, field notes, courtesy of T. Giermakowski). During the 1980's, Richard Felger reported that tortoises were prized as food (Felger et al. 1981), and that even mud turtles were also regarded as food (pers. comm., 1987). The Seri tribe historically ate tortoises in substantial numbers, and though today turtles are reportedly consumed for ceremonial purposes and thus in very small numbers (Nabhan 2002, 2003), we suspect that they are still used opportunistically as food by some of the local people.

During the 21st century in northern Sonora, some biologists and naturalists working in Sonora report that many people still eat tortoises, while other observers report the opposite. We found few residents outside northern Sonora who self-reported eating tortoises, and got very few reports of tortoises still being used as human food. Most people, even outside cities, appear to be aware that tortoises are protected, which may have made them reluctant to tell us they are being eaten, but this was not apparent in the tenor of conversations.

In the TDF region of Alamos, at least six informants provided consistent, convincing reports that eating tortoises now (2012-13) is essentially not done at all: generally, these informants indicated that up to 10 or more years ago a few older people still ate tortoises, which was more common decades ago. Forest products are still widely used in the TDF, including harvest of many tree species (Felger et al. 2001), but it appears that many of the local people are aware that tortoises are protected and are part of a natural patrimony. It appeared to us that most people were also aware that this natural patrimony has benefits in providing current and future jobs in ecotourism and natural resource conservation. In relatively remote areas south of El Fuerte, Sinaloa, our group, initially mistaken to be involved with the narcotics economy, was recognized as being like people they had seen on the Animal Planet television channel.

In tropical thornscrub at Suaqui Grande in east-central Sonora, an informant told us that people ate tortoises, but only or predominantly in the past; there was some indication that it might still rarely be done, but the larger effect was people keeping them in yards, apparently as pets, from which they escaped. Farther north in more arid thornscrub at Mazatán, we learned that eating tortoises was still frequently being done, primarily involving tortoises opportunistically found crossing roads; at Ejido El Opodepe near the northwestern, arid thornscrub margin, our group of ≈12 experienced searchers only located a single tortoise. It is possible that people living in poverty at some locations in the countryside of northern and north-central Sonora still eat tortoises with some regularity, although the Mazatán report was the only direct evidence we received of it in thornscrub.

Southwest of Caborca in the Sonoran Desert, informants reported that a single, poorly paid cowboy on a remote ranch regularly ate tortoises, possibly totaling up to 40-50 per summer. At other less remote ranches in the Caborca region, many of which are used primarily as hunting and conservation reserves, we had no reports of tortoises being used as food, although all personnel were familiar with tortoises and saw them frequently.

In summary, it is clear that tortoises are still used as food by humans living north of the TDF and Alamos region, but this appears to be rare or uncommon, and highly localized. It is highly likely that this is far less common than previously reported. With continued economic development in northwestern Mexico, we confidently predict that significant use of desert tortoises as human food will be a historical phenomenon in the foreseeable future. As such, use of desert tortoises for food can be recognized as an impact but not a threat of extinction.

1.3.4 Road Mortality

Road mortality and collection of desert tortoises crossing paved roads and major graded dirt roads are well known in the Mojave Desert (Baepler et al. 1994; Berry and Turner 1987; Boarman 2010; Boarman and Sazaki 1996, 2006; Boarman et al. 1997; Karl 1989; LaRue 1993; Nicholson 1978; von Seckendorff Hoff and Marlow 1997, 2002). It has been shown repeatedly to have a depletion effect extend detectably to 1.6 km (reported ranges of 0.3 – 4.6 km). Boarman and Sazaki (1996) suggested that this results in a preponderance of juvenile tortoises in the depletion zone, which we have also observed in the Sonoran Desert at Organ Pipe Cactus National Monument (Rosen and Holm, *manuscript*).

Similar data are not available for desert tortoises in Mexico, but population depletion near major roads is certainly occurring. Density of paved roads and traffic intensity are generally much lower and lower, respectively, in northwestern Mexico compared to the United States. There are, however, a large number of heavily used improved dirt roads in tortoise habitat in Mexico, and density of both paved and improved dirt roads is increasing rapidly now.

Our observations on this issue are limited. In remote areas near Sierra El Viejo, desert tortoises are common to very abundant on unpaved roads. Within the fenced, controlled confines of the ranch we worked on near El Plomito, numerous very rough roads have been made to facilitate access for deer hunting. At suitable times, we found ≥ 1 tortoise per km, the animals taking advantage of the smoother access compared to often extremely cobbly conditions on surrounding bajada environments. Travel in August and September on dirt road thoroughfares connecting this ranch and other interior ranches with major roads to Caborca often yielded 1-3 live tortoises, all juveniles and immatures, even though the environment is sandy and > 1 km from rocky slopes and bajadas. Informants told us that numerous tortoises used for food had been collected primarily on this and other area roads. We have seen tortoises on paved roads east of Hermosillo, near La Colorada, Mazatán, Moctezuma, and Baviácora, particularly on less heavily travelled roads such as near Baviácora. These data are radically different from essentially all experience on more heavily traveled roads, and most highways in the United States, and give a rough idea of how abundantly tortoises may seem on roads before populations adjoining roads are depleted or extirpated.

Similarly, in the Alamos, Sonora region, tortoises are rarely found on roads near the town, as they were 15-20 years ago, whereas we found them on more remote roads to the east in and near Reserva Monte Mojino. These observations, although anecdotal, confirm an expectation that road effects on desert tortoises are severe and likely are similar to those in the United States in depleting populations for some distance away from road edges. In Mexico, however, tortoises were until recently widely collected for food, and are still likely more frequently collected as pets than they are in the United States. Thus, we suggest that current and pre-existing road effects in Mexico are the result of a different pressure. Instead of (or possibly in addition to) road kills, animals are collected for pets or food in Mexico, whereas roadkills and collection as pets are, or have been, more common in the U.S. The results along some Mexican roads may equal or exceed those in the U.S. Road effects in Mexico will continue to be a conservation problem for tortoises as paved and improved road networks are upgraded and extended to new areas currently occupied by tortoises.

1.3.5 Disease

We tested blood and nasal lavage samples from 69 wild and 22 captive tortoises from Mexico for *Mycoplasma* bacteria or antibodies using ELISA, cultures, polymerase chain reaction tests for detection of *Mycoplasma agassizii* and *M. testudineum* (Berry et al., *in press*) Among wild tortoises, there was only a single, questionable positive serology test from a tortoise at Rancho El Bámuri, a remote site south of Caborca (see Berry et al., *in press*). We found little sign of disease in wild tortoises during 2005-2013, but during a major mortality episode and population decline in the Tiburon Island region observed in 2001-02 (see Chapter 3), several tortoises on the coastal mainland near Punta Tepopa were ill with upper respiratory tract disease (URTD), albeit of unknown etiology. In contrast, 15 of 22 captive desert tortoises at Centro Ecologico de Sonora (CES) in Hermosillo tested positive for *Mycoplasma*, and these and other captives pose a threat of disease spread by release to the wild (Berry et al., *in press*).

Although not clearly demonstrated, captive tortoise release in California may be primarily responsible (Jacobson et al. 1995, 2013) for the deadly *Mycoplasma* epidemic that has been associated with population declines of *G. agassizii* in Mojave Desert (Christopher et al. 2003). The disease is reported to have been first in evidence in proximity to human activity including at Desert Tortoise Research Natural Area (DTRNA) in the western Mojave Desert, where captive tortoises have sometimes been released by the public (Jacobsen et al. 1995; Berry 1997). The incidence of this pathogen in *G. morafkai* in Arizona, although low and not associated with disease, has some relation with proximity to cities (Dickinson et al. 2001, 2002, 2005; Jones 2008; Jones et al. 2005).

In some respects, disease effects show similarity to other impacts associated with proximity of human settlements to *G. agassizii* in California (Berry et al. 2006; Esque et al. 2002) and *G. morafkai* in Arizona (Zylstra et al. 2012). It is not entirely clear whether these proximity effects are due to exotic disease introduction, collection or shootings by humans, injuries caused by domestic dogs, incidental stress to the tortoises by presence of humans and their animals, attraction of natural predators such as ravens and coyotes (Esque et al. 2010) to resources created by human settlements, a combination of some of these factors, or other unknown impacts.

As yet, neither disease nor other human-proximity effects have been shown to occur in Mexico, with the exception of the highly populated Hermosillo. Tortoises were abundant and apparently healthy at La Pintada, the most accessible to urbanites among our sampling sites, where we confirmed the presence of formerly captive tortoises. By contrast, the site near Punta Tepopa, where ill tortoises were found, is very remote and unlikely as a release point for captives, although the Seri have reportedly moved tortoises around and, historically, consumed them in significant numbers. The El Bámuri site is also remote and not a likely target for release of tortoises moved long distances or from crowded captive conditions in which disease may proliferate or be vectored by exotic chelonians

If *Mycoplasma* disease is caused by an exotic pathogen, which has been suggested (Jacobson et al. 1995) but not demonstrated (Jacobson et al. 2014), rather than a native infection with drought-related virulence, its escape into *G. morafkai* populations, which would seem to be inevitable, would be more strongly predicted to be a major threat. The absence of epidemic and fatal *Mycoplasma* disease in wild *G. morafkai*, suggests it may not be a very likely threat, particularly as it has no demonstrated association with the several major population declines known in the species. At present, we can conclude that disease is not a demonstrated or presumptive threat to *G. morafkai* anywhere, but the mystery of the origin and modes of virulence of *Mycoplasma testudineum* and *M. agassizii* implies that it may be a threat that could emerge. As an ultimate or primary proximate cause of widespread mortality or threat to the status of *Gopherus* species, disease remains enigmatic.

1.3.6 Habitat Destruction

Habitat loss is the most often sited cause of species decline and biodiversity threat. Although it pales before the several other factors threatening desert tortoises, it deserves description as a general phenomenon.

1.3.6.1 Urban Sprawl

Hermosillo is a rapidly growing and industrializing city that in the next several decades may expand to the north and east across mountainous regions where tortoise habitat may be affected. It is already in contact with low mountains with suitable tortoise habitat at its north and south ends, with associated effects (e.g., collections, disease proliferation, dog predation) on tortoises but unknown effects on populations. Depending on the amount of human population growth in Mexico, several other towns and cities including Sonoyta, Pitiquito, Benjamin Hill, Punta Chueca, Kino Bay, Moctezuma, San Carlos, and Obregon could expand to have impacts on significant areas of tortoise habitat, although none of this is a large threat in the more immediate future.

It is presumed, based largely or entirely on anecdotal reports, that *G. morafkai* is extirpated by suburban sprawl where it occurs over bajada habitat and up into rock slopes. We have a report (I. Valle, J. Verdugo, pers. comm. 2013) that tortoises occur in habitat in the south edge of metropolitan Hermosillo, and in Tucson in low abundance in the middle bajada of suburban Tucson Mountains (C. A. Lowe, pers. comm., 2003), and they are still seen occasionally (at least) on upper bajada and foothills of Tucson Mountains (pers. obs., P. Rosen). Although a population occurs on Tumamoc Hill in central Tucson (T. Edwards, pers. comm; P. Rosen, pers, obs.), it may be sustained entirely by released or escape of captive tortoises, and has not been studied demographically. However, these lines of evidence are

not necessarily convincing. The Tucson Mountain middle bajada population declined to virtual extinction within 2-4 decades of suburbanization (C.H. Lowe, pers. comm., 1999); and tortoises present on the bajada may be escaped pets, transient migrants, or all that remains of vanishing populations. In Santa Catalina Mountains bajada north of Tucson, desert tortoises are rarely seen, and are reported to have disappeared from highly suitable habitat during the past 3-4 decades (J.T. Bagnara, pers. comm. 2012). Demise of tortoise populations is reported in mountain parks with native vegetation in urban metropolitan Phoenix.

Zylstra et al. (2012) reported that proximity to incorporated communities in Arizona was a significant contributor to mortality rates in *G. morafkai*. Likewise, Berry et al. (2006) and Esque et al. (2010) demonstrated negative effects of proximity to human communities in *G. agassizii*. Thus, although there is some ambiguity, data suggest and considerations of multiple urban-related impacts supports a determination that desert tortoise populations in Sonoran Desert have not proven viable under the effects of suburban sprawl. The primary causes of loss of suburban populations in areas where domestic dogs are usually not running loose are probably collection as pets and, in the past for sale (J.T. Bagnara, pers. comm.). Tortoise populations could be restored in such areas, although probably only under priorities set by ESA listing, and concerns about vectoring disease from exotic reptiles to restored tortoise populations and thence to existing wild populations would be a concern (Edwards and Berry 2013).

1.3.6.2 Agriculture

Agriculture, in the sense of row-crop production and irrigated pasture (see Fig. 3), also has somewhat limited effect on desert tortoises in Mexico. This agriculture was intensively developed starting in the 1940s west of Hermosillo and through the 1960s west of Obregon, resulting in almost total loss of rich desert and riparian woodlands by the late 1970s (Búrquez and Martinez-Yrizar 1997). However, these most affected areas are large, flat, river deltas with, so far as known, little or no potential suitability as tortoise habitat. However, Van Devender et al. (2002) reported tortoise records in non-rocky areas of southern coastal Sonora: if these represent unknown populations with unexpected habitat association, the potential and past impacts of agriculture on desert tortoises in Mexico will need to be reconsidered.

A likely much larger impact associated with both large-scale irrigation agriculture and the growth of large cities is installation of major dams in mountainous areas occupied by desert tortoises, as on the Salt, Verde, Gila, and Colorado rivers in Arizona and the ríos Sonora, Yaqui, Bavispe, Mayo, and Fuerte in Mexico. Much of the damage is likely already done.

1.3.6.3 Mining

Mining is widespread in the Sonoran Desert region, with large open pit operations being established currently in or near tortoise habitat near Tucson, Safford, and Superior, Arizona, and near Quitovac, Sonora and Chinipas, Chihuahua, and undoubtedly in many other places. Existing mines have permanently eliminated much tortoise habitat in many places, including Tucson, Marana, San Manuel, Mammoth, Kelvin, Hillside, Ajo and elsewhere in Arizona, and Quitovac, Moctezuma, Alamos, and elsewhere in Mexico. The irreversibility of mining and the apparently relentless increase in demand and

destructiveness of impact entailed make mining a potentially serious long-term threat to tortoise populations.

1.3.6.4 Desert Shrub-tree Harvest

Harvest of desert trees for fuel wood, charcoal, construction and furniture, and artisan carving has seriously damaged Sonoran Desert woodlands in local areas over a significant part of the Sonoran Desert of Mexico (Nabhan and Carr 1994). This removes important thermal-buffering shade (Grandmaison et al. 2010; Lagarde et al. 2012) and may aggravate heat- and drought-related physiological challenges in *G. morafkai*. However, the die-offs and population decline we found in the Seri lands (Chapter 3), which are an area of significant desert tree harvest, were not evidently related to any visible deficit of expected tree density. Thus, the importance of this impact for tortoises is not currently supported by any evidence. This harvest is no longer unregulated in Mexico, although the effectiveness of regulation and the overall severity of tree and shade depletion remain unknown.

1.3.7 Livestock Grazing

Livestock grazing, primarily involving cattle and sheep, is almost invariably cited as an important negative effect on desert tortoises. It is obviously a plausible impact via competition for food plants, and may facilitate replacement of palatable, nutritious plants by less beneficial and often exotic plants. It is expected or predicted that under challenging physiological conditions such as drought and climate change, the competitive effect of livestock on tortoises might cause a tipping point to mortality and might, under less extreme climatic conditions, affect growth and reproductive output. More importantly and subtly, the long-term changes engendered by grazing, especially the elimination of perennial grasses, may be critical in tortoises' ability to withstand drought periods. However, the presumption that reduction of perennial grass cover is purely detrimental to tortoises has not been rigorously discussed. Reduction in perennial cover may benefit forbs, some of which are among the highest quality forage items for tortoises (Oftedal 2002; Oftedal et al. 2002). Further, effects of grazing on desert tortoises are poorly demonstrated (Avery and Neibergs 1997), and there are no definitive data demonstrating changes in population status of desert tortoises either after grazing cessation or via this dietary mechanism in the field. Desert tortoises have persisted in livestock pastures for several centuries. Inasmuch as major conflict with ranching interests over this issue would be highly detrimental to both sides, the issue should be subjected to rigorous study, which it has not.

In Sonora, the single known catastrophic decline of desert tortoise populations occurred on Isla Tiburón, a protected area with no livestock grazing, and on the nearby coastal mainland where cattle grazing exists. Earlier episodes of catastrophic mortality in Sand Tank and Saucedo Mountains, Arizona, also occurred in areas closed to livestock grazing. Although consequential competition of desert tortoises with livestock for forage has not been demonstrated, further research might change this.

A serendipitous outcome of grazing appears to be a decrease in human predation on tortoises as beef became readily available in northwestern Mexico, and as ranch hands (often) received sufficient monetary compensation to afford beef and other meats.

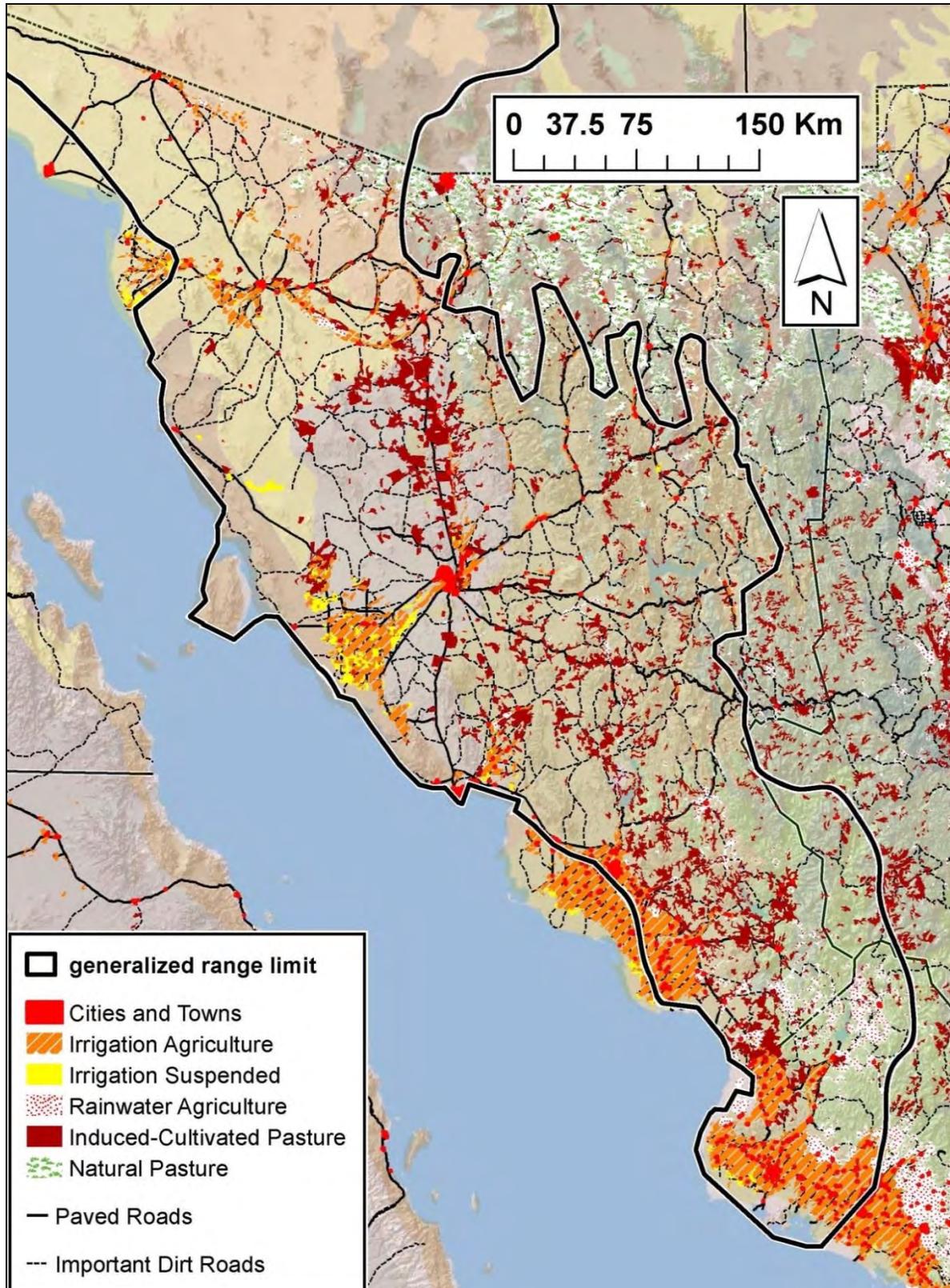


Figure 1.3. Urbanization and agricultural threats to the Sonoran Desert tortoise in Mexico based on INEGI (2000) GIS data layer for Mexico. Biomes color coded in background are equivalent to those in Figs. 1.1 and 1.2.



Figure 1.4. Primary (top) and secondary (bottom) tropical deciduous forest at Rancho El Guayabo, Reserva Monte Mojino, Alamos, Sonora, 24 August 2013. Tree species diversity in primary forest is evident as uneven color and height of the vegetation, whereas the secondary forest, which has replaced induced pasture in ca. two decades, retains a lower tree diversity of species that are rapid invaders.

In the TDF, buffel grows densely and abundant in cleared pastures and is similarly desired as a way to greatly increase livestock carrying capacity. Virtually all lowlands vales among hills and mountains in the Alamos region, including far to the east in the TDF of the Reserva Monte Mojino (ReMM), have been stripped of TDF and planted with buffel during the past 2-4 decades – as well as converted to cropland where slope and soil permit. However, TDF tree species rapidly invade pasture, which must be repeatedly cut to prevent re-establishment of forest, as seen in ReMM after just ≈ 2 decades of abandonment (Fig. 4). Even with maintenance, sustaining monocultures of buffelgrass appears to be quite difficult, with a rich native forb flora becoming dominant (Fig. 5). Nonetheless, it is present in small, dense stands in some exposures in primary natural TDF in the Alamos region. Further, in the Alamos region, some buffel pastures have recently been invaded by alien plants resistant to fire effects and unpalatable to livestock (M. Figueroa, pers. comm. 2012). As such, changes in management regime can apparently readily reverse the buffel invasion in TDF, and thus buffelgrass is not necessarily an existential threat to the TDF.

The most serious problem associated with livestock grazing and ranching is habitat modification via the introduction and spread of exotic grasses to enhance range capacity.

1.3.8 Buffelgrass

Buffelgrass is a coarse, hardy Old World perennial bunchgrass widely introduced in northwestern Mexico, especially Sonora, and actively spread by government and private efforts. It is reported to increase livestock range capacity by at least threefold (Hanselka and Johnson. 1991; Búrquez et al. 2002) and as such is difficult to combat in an economy driven by beef cattle production. The reasons for buffelgrass's great success are not all entirely clear, although it is presumed that in the absence of many of its native enemies, which might include natural grazing regimes, rodents, insects, and microbes, it has an invader's advantage over native plants. It forms denser clumps than most native grasses (possibly excepting *Heteropogon contortus*; pers. obs.), and thus carries catastrophically hot fires that damage and can extirpate native woody perennials. Alternatively, it may have superior adaptations or exaptations compared to the native grasses, thus more successfully growing strongly and spreading into desertscrub.

An important facet of this problem is the precarious balance between desertscrub and grassland (semi-desert grassland) throughout much of less arid, biologically rich Sonoran Desert and arid thornscrub of Arizona and Sonora. Rainfall amounts are close to that required for the natural transition between desertscrub and semi-desert grassland throughout much of the region outside the LCV and Central Gulf Coast phytogeographic provinces of the Sonoran Desert in Arizona and Sonora. In a classically ironic statement (Smith 1910; Thornber 1910) noted that the grasslands of the Tucson region were all but useless for livestock because they were so easily transformed to desertscrub grazing, as McAuliffe (1995, 1997) has demonstrated elsewhere in Arizona's Sonoran Desert. It is also possible, therefore, that decimation of the grass communities in desertscrub and thornscrub under historic overgrazing has cleared the way for buffelgrass success.

Shreve (1951) recognized, and a casual drive-through makes clear, that the Plains of Sonora phytogeographic province of the Sonoran Desert surrounding Hermosillo (see Figs. 1 and 2) was rich in grasses and could be a type of desert grassland, or arid savannah, under lower grazing pressure (Búrquez et al. 1998). This is the core area of buffelgrass's threat to the native woody shrub ecosystem of the Sonoran Desert (Fig. 3). However, even in the relatively level valley floors of the Plains of Sonora, where buffelgrass is clearly at its strongest, it is apparent that diversity and abundance of native ephemeral and perennial grasses are still present. This suggests that in the absence of heavy grazing pressure and with active management, certain local and regional areas within the Sonoran Desert might be native Sonoran semi-desert grasslands. This, combined with the advantages buffel appears to have, indicates that the threat of buffelgrass in the Arizona Upland and Plains of Sonora is not only likely to continue, but may be very difficult to reverse.

In contrast, other regional subtropical aridlands are or may be less threatened by buffelgrass. Although the species grows in arid LCV environments, and can become dominant in small areas, it does not dominate larger plots or areas in this region. It is a weak invader of intact desertscrub in valley flats of the Tucson region, although extremely invasive in disturbed areas from which creosotebush has been



Figure 1.5. Induced pasture at Rancho El Palomar, Alamos, Sonora, 19 October 2012, showing rapid invasion with native forbs (top) and trees (bottom). Non-native buffelgrass is visible at lower left (top) and lower half (bottom) as the yellow-green plants.

removed (P. Rosen, pers. obs. 2006). We have observed desert pastures between Caborca and Altar in which it was apparent that maintaining buffelgrass in the desert may require repeated treatments of re-seeding and shallow ploughing. In this region and elsewhere in the Sonoran Desert region, monoculture stands of buffel are prominent along disturbed highway margins, along which the species spreads and in which people are frequently seen in Sonora harvesting seed for maintenance or expansion of “induced

pasture” in desertlands. Within the range of *G. morafkai*, buffelgrass is less invasive in the more arid biotic communities that are, unfortunately, also less suitable for the tortoise.

Although buffelgrass pastures may be quickly restored to low-diversity TDF, and eventually reacquire the high biodiversity of TDF, its recent extensive use in conversion of forest to pasture has impacted the Sinaloan tortoise. We initiated monitoring of operative temperatures (the temperature an animal would achieve in various parts of its environment) in the Alamos region using models of tortoises containing temperature data loggers. Results from the first year showed that TDF thermal regimes were suitable for tortoises during most of the day throughout the tortoise active season, and even during most of the dry season when leafless trees allow sunlight to penetrate to the dry forest floor. However, in converted pasture, operative temperatures exceeded the thermal activity limits for desert tortoises (Zimmerman et al. 1994) for most of the warm season, with hours of activity restriction (h_r , a measure of high-temperature impacts on reptiles [Sinervo et al. 2010]), at ≈ 5 hours/day from March-October and ≈ 8.5 hours/day in July and August). Buffel conversions transform the thermal environment to desertscrub conditions. In contrast, h_r in TDF was less than 2.5 hours in any month and averaged ≈ 0.75 hours during March-October. In TDF, tortoises were essentially freed from constraints of high temperature, as they could essentially always find thermally suitable foraging habitat in large parts of the forest environment.

In October, the operative thermal environment in converted pasture became suitable for tortoises (in fact, in late October-November, warm temperatures in pastures may be preferred over thermal regimes in the forest prior to leaf-fall. In October, as predicted by the operative temperature data, we found tortoises in the pastures surrounded by hills with primary TDF, where we found many tortoises in August through October. We found a few small juvenile tortoises in tracts of primary and secondary TDF in the Alamos region, but not in the area of mixed pasture and TDF we studied.

In TDF, therefore, buffelgrass appears to severely damage tortoise habitat, although seasonally it becomes suitable for tortoises. Further, although restoration of native TDF is possible where the will exists, there remain strong economic incentives in favor of buffel, and the ultimate balance between TDF and induced pasture will be determined by legal protections and the relative benefits of ecotourism, forest products, and livestock grazing.

It is less clear how buffelgrass functions within Sinaloan thornscrub, where it is also present and managed. In mesic thornscrub east of Navajoa, visible along the highway to Alamos, buffelgrass pastures are obviously being overgrown by boat-thorn acacia (*A. cochliacantha*), but it is not clear that this process occurs similarly elsewhere, especially in more arid expressions of Sinaloan thornscrub in Sonora. At sites we surveyed in mapped thornscrub north-northeast of Obrégon, Sonora, buffelgrass was less common and more local than in Plains of Sonora and TDF, including where thornscrub was cleared for livestock. Other plants, annual forbs and grasses and other perennial grasses and re-invading native woody perennials were more prominent than buffel. Whether the native plant biodiversity in pastures in Sinaloan thornscrub will resist the buffelgrass invasion or the thornscrub can successfully reclaim induced pasture are not clear. Most of the thornscrub sites where we found dead tortoises were not influenced by clearing of native vegetation for pasture.



Figure 1.6. El Batamote buffelgrass invasion site, 47 km N of Hermosillo (see Esque et al. 2002; Bury et al. 2002) in 2003 (above) and 2013 (below). Scale bars at lower left represent 3.8 km. Valley is heavily occupied by induced pasture (yellowish-brown) while rock slopes support tropical thornscrub-like vegetation. Changes are not obvious at this scale, suggesting that changes over 10 years have not been profound.

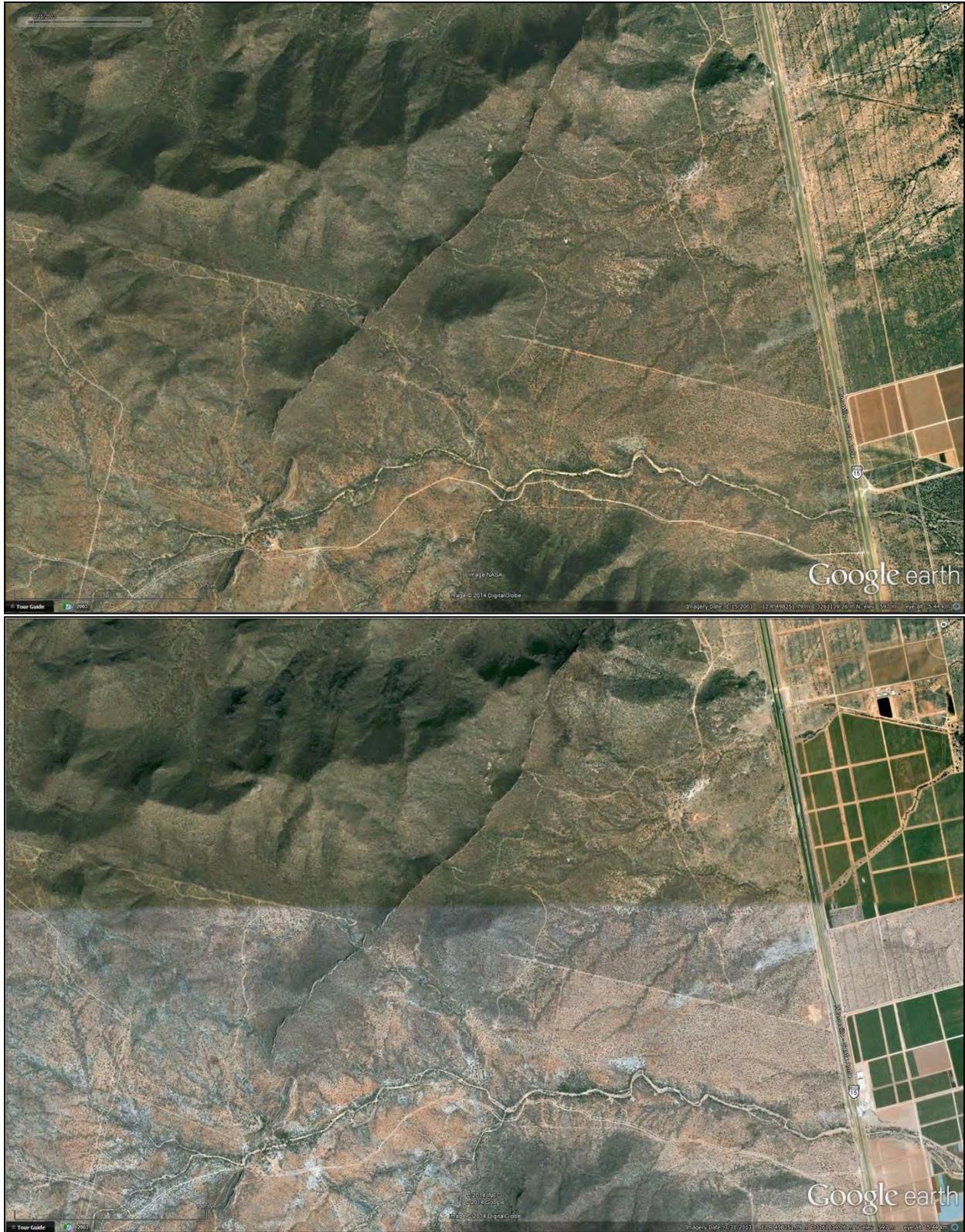


Figure 1.7. Same area and time profile as 6.A, zoomed in with scale bar representing 1111m. Increase in pasture at the expense of thornscrub are visible in and above the lower-left quarter of the lower image, which can be confirmed by closer imagery (next image set).



Figure 1.8. Same area and time profile as Fig. 6A zoomed in to lower center of Fig 6B, with scale bar representing 451m. Increase in pasture at the expense of thornscrub appears to have occurred at a hectare or larger scale and to be advancing toward the diagonal ridge in the upper left quadrant.

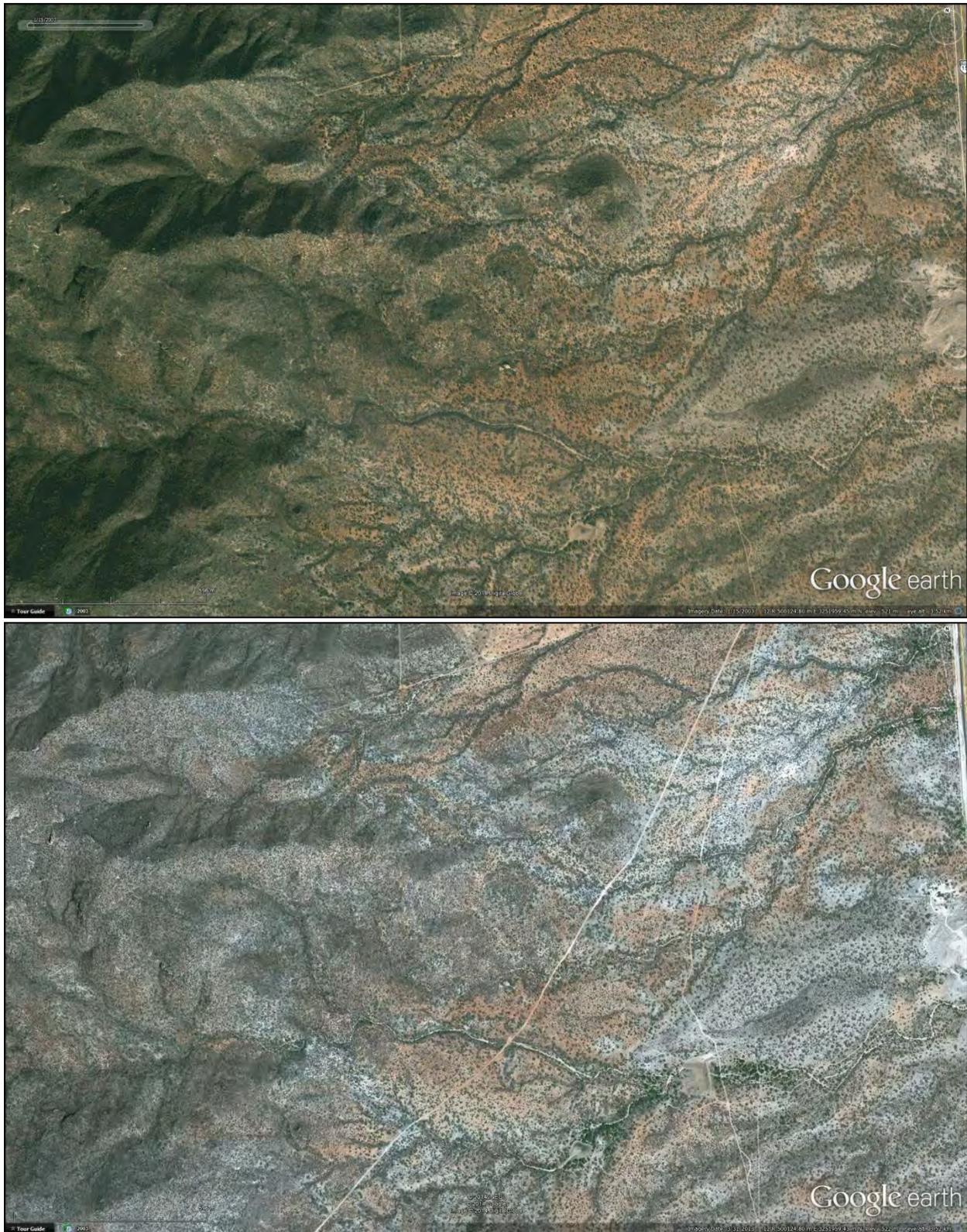


Figure 1.9. Another example (2003 above, 2013 below), from just E of Agua Salada (“La Salada”), ca. 20 km S of Batamote, also in the Plains of Sonora. Scale bars represent 596 m. Expansion of induced pasture is not apparent at this locality, although both localities are represented by the same seasonal aerial imagery series.

Although buffelgrass is not a severe and apparently ubiquitous threat everywhere in the region, as it is in the valleys or the Plains of Sonora and hills of the Arizona Upland (Búrquez et al. 2002; Van Devender and Dimmitt 2006), and although there are auspicious signals of native vegetation resilience to buffelgrass takeover, the threat remains extremely serious and without clear solution for affected areas. From the standpoint of buffel as a long-term threat to the desert tortoise, two pivotal issues are the trajectory of buffelgrass spread and its impact on native vegetation, which the foregoing discussion shows to vary sharply among the three biomes, and the depth of buffel impacts on tortoises and tortoise populations..

There is limited but highly concerning evidence demonstrating mechanisms of buffelgrass effects on desert tortoises. Esque et al. (2002, 2003) demonstrated that desert tortoises are killed in at least moderate numbers in fires carried by buffelgrass, although Wirt et al. (1999) found tortoises still abundant on one of Esque et al.'s post-fire tortoise survey sites. Esque et al. (2002, 2003) also noted that fires spread by buffel (and other exotic grasses in United States) kill trees and other shade plants, altering the thermal regime and shelter availability for tortoises. Our operative temperature studies in Sonora (Chapter 6) show that induced pasture is much less thermally favorable for tortoises than TDF for most of the year, although dense buffelgrass offers thermal buffering that, while poor relative to the forest, is similar to thermal regimes in desertscrub. In TDF, full conversion to induced pasture would lead to the extinction of tortoise populations; the effect in thornscrub would be less clear cut but might vary according to degree of aridity and tortoise genotype.

Of equal or greater concern is Gray's (2012) report that *G. morafkai* in study plots heavily infested with buffelgrass had condition factors (Body Mass Index [BMI]: [body mass] / [shell length X width X height]) about 10% lower than those in similar nearby areas with little or no buffel. Although BMI is not as good a predictor of *G. agassizii* health and stress as blood chemistry (Peterson 1994, 1996a&b) the amount of decrease in Gray's report is similar to that found in physiologically stressed tortoises in Peterson's study in Mojave Desert. Gray's (2012) study was observational and comparative, rather than experimental, and did not explicitly consider whether buffel abundance varied for correlated environmental, rather than history-of-invasion, reasons. Nonetheless, Gray's (2012) proposed mechanism for the buffelgrass effect is cogent and convincing: reduced food quality and quantity (see Olsson et al. 2012a) available to tortoises. Under climatic and dietary stress, this proposed mechanism, based on the observed reduction in body condition, would likely make *G. morafkai* vulnerable to physiological stress, and both survivorship and reproduction could be affected. Considering these observations and causal pathways, the continuing buffelgrass invasion poses a potentially serious, growing threat to *G. morafkai* in desertscrub and thornscrub, particularly if it acts in combination with climatic change.

Olsson et al. (2012b) demonstrated that buffelgrass is continuing to rapidly expand its local distribution in foothills and lower mountain slopes near Tucson. Along Ajo Way, buffelgrass has extended its visible roadside abundance over 100 km west from Avra Valley to the eastern half to Gu Oitag Valley in less than a decade (P. Rosen, pers. obs. 2014) and is increasing on hills with suitable tortoise habitat along the road near Sells. Bury et al. (2002) reported that buffelgrass, with and aided by its enhanced fire regime, is spreading into rocky environments at a known *G. morafkai* locality (El Batamote) in the Plains of Sonora. Buffelgrass has been more widely established in Sonora than in Arizona through intensive

government sponsorship (Búrquez et al. 2002; Van Devender and Dimmitt 2006) but there is little published evidence of its current rate of spread from valley pastures into core tortoise habitat in Plains of Sonora. Búrquez et al. (2002) showed that natural hillsides in the Plains of Sonora had the lowest representation of buffelgrass among many local environments they sampled, but arroyo margins were among the most heavily infested local environments. High resolution aerial imagery available on Google Maps is available for El Batamote (but few other sites of concern here), and indicate that buffelgrass is indeed continuing to spread there (Figs. 1.6 – 1.8), but not at another similar site (Fig 1.9). A vast area of interior desert mountain ranges in the Plains of Sonora has not been surveyed for tortoises (Fig. 2), as access has proven difficult.

Much of the range of *G. morafkai* with Sonoran (as opposed to Sinaloan or mixed) mtDNA haplotypes and nuclear microsatellite genes is in the Plains of Sonora, and more is in the Arizona Upland biotic community in Mexico and the United States. These comprise the core habitat of *G. morafkai* (in the strict genetic sense), which is therefore potentially under critical threat from buffelgrass. Additional research is required to (1) confirm the severity of threat at the demographic and population level, (2) evaluate the degree of vulnerability of *G. morafkai* habitat, specifically, to buffelgrass invasion and persistence, especially throughout the Plains of Sonora, and (3) develop a conceptual basis for containing, managing, and mitigating this threat.

1.3.9 Habitat Fragmentation

Habitat fragmentation in desert tortoises by major linear and large-area features, primarily anthropogenic, is likely to be caused principally by highways, railways, canals, modern large-scale irrigation agriculture, and urbanization. All of these features are present in northwestern Mexico within the range of *G. morafkai*. All have increased greatly during the past 5-7 decades, and at least one (paved highways; see Fig. 3) is increasing rapidly now and can be expected to continue to do so in coming decades. Although collectively, habitat fragmentation, especially by linear features such as highways and railways, is a significant threat to mortality and genetic exchange, large-area threats (agriculture and urbanization) are likely to lead to more complete habitat fragmentation. Tortoise population losses in islands of rocky habitat areas surrounded by urbanization and agriculture, where immigration and emigration are eliminated, and other direct effects of human proximity occur, are most likely to face local extinctions. Linear feature habitat fragmentation has a lower potential for short-term population extinctions, and may in the future be manageable for high-profile animals such as desert tortoises using translocations guided by genetic research. Regardless of habitat fragmentation or continuity, under projected climate warming and drying habitat change may be so rapid that plausible management to save the species will include translocation on even larger scales.

1.3.10 Vandalism and Predation

Vandalism of desert tortoises by shooting is well-known in *G. agassizii* in the United States, especially in Mojave Desert, where it is reported as a notable cause of mortality at several localities and continuing over a number of decades (Berry 1986, Berry et al. 2006). We consider this unlikely in Mexico, in the absence of evidence that it occurs, and also for sociological reasons.

Predation has significant effects on desert tortoise populations (Averill-Murray et al. 2002b; Medica and Gregor 2009; USFWS 2010, 2011), including predation by natural and domesticated animals. This is most clearly portrayed in survivorship models by Zylstra et al. (2012), who found that *G. morafkai* survivorship was lower in less arid than more arid study areas except in drought times (when survivorship was lower in arid environment populations). This was related to the numerous reports of carcasses showing damage attributed to mountain lion predation. Greater importance of predation, as opposed to drought, in less arid sites (Zylstra et al. 2012) may be critical with respect to both the mesic range limits and the potential for climate change adaptation via range extension in desert tortoises.

The jaguar, which occurs in large parts of the more remote thornscrub and TDF inhabited by desert tortoises in Mexico, is a large cat that is known to prey on tortoises (Emmons 1989; Garla et al. 2001). Jaguars and mountain lions coexist in TDF and the combination may increase predation pressure on their prey species (Nuñez et al. 2000). Conservation efforts in favor of such large cats might affect tortoise demographics and abundance. Carnivores are more diverse in TDF than in Sonoran Desertscrub: 6 versus 2 felid species; approximately 20 versus 12 carnivore species total (Ceballos and Martinez 2010; Hoffmeister 1986; Schwalbe and Lowe 2000). In this diverse assemblage, about a third of those reported in TDF occur primarily well south of the range of *G. morafkai*, while about half of those in desertscrub are marginal or largely restricted to riparian areas that have limited proximity to *G. morafkai* (Ceballos and Martinez 2010; Hall and Kelson 1959; Cockrum 1964; Hoffmeister 1986). Smaller predators of tortoises, such as snakes, beaded lizards, and birds are also more diverse, and probably more abundant, in TDF than in desertscrub. In the urban-influenced south outskirts of Hermosillo, predation by raccoons and sometimes foxes has been a problem with captive desert tortoises held outdoors at CES. The diverse predator assemblage of more tropical environments in the region likely influences tortoise abundance and distribution. It has been speculated that the southern range limit of desert tortoises, which is in the northern, drier extent of TDF, may be related to fungi and pathogens (Bury et al. 2002; Van Devender et al. 2002). Predation has not previously been suggested as the southward limiting factor in desert tortoise distribution.

Predation or killing of tortoises by domestic or feral dogs (*Canis lupus familiaris*) is also well known in the United States. It is associated with human settlements and may contribute to reduced survivorship attributed to proximity to human settlements (Bjurlin and Bissonette 2001; Zylstra et al. 2012). We have no information on whether this may be commonly occurring in Mexico, but domestic and ranch dogs are rarely well fed or fed at all, so it is conceivable that their impacts on local tortoise populations along the edges of settlements and on ranches may be significant.

1.4 SUMMARY AND SYNTHESIS

Our survey of the distribution, abundance, and conservation status of *G. morafkai* in Mexico was in some respects encouraging. We found live tortoises at virtually every site we surveyed within their geographic, elevational, and macrohabitat limits (Fig. 1) including areas chosen without information on tortoise occurrence. Places within the range where we did not find them were not sampled extensively. In many locations, particularly in TDF, in the Hermosillo region, and both northwest and southwest of Caborca, it was apparent that tortoises were abundant to very abundant. In TDF, we found good

evidence of steady recruitment into adult size-age classes as well as reliable reports that human predation on tortoises has declined and is, at least locally, a thing of the past. While people are still eating tortoises in some areas elsewhere in Sonora, it is localized and at substantially lower frequency than three decades ago. We note potential negative effects of grazing, and severe effects of habitat modification to favor grazing. However, there is a positive trend to establish many private ranches as hunting and conservation reserves (“UMAs” - Unidad de Manejo para la Conservacion de Vida Silvestre [<http://www.biodiversidad.gob.mx/usos/UMAs.html>]) throughout much of *G. morafkai*'s distribution in the Sonoran Desert in Mexico. We found limited evidence for road mortality impacts in the landscape overall and very limited evidence of diseases such as mycoplasmosis that appear to be contributors to the declines of *G. agassizii* in Mojave Desert. Even close to Hermosillo, *G. morafkai* is present, and not far away it seems to be abundant. Finally, despite several serious threats and impacts, we found no evidence of extinction of any population of *G. morafkai* outside of major urban areas where anecdotal evidence in the U.S. does suggest local extinctions.

There are, however, at least two major threats looming over the immediate future of *G. morafkai*, buffelgrass invasion and anthropogenic global warming. Buffelgrass invasion is a potentially intractable, growing problem because (1) buffelgrass greatly increases range productivity for cattle, giving it an economic imperative, and (2) the grass has and clearly continues to self-spread into prime tortoise habitat in Arizona Upland and Plains of Sonora deserts scrub and at least into some, if not many habitat areas in Sinaloan Thornscrub. Population effects of buffelgrass on *G. morafkai* have not been demonstrated, but mechanisms of impact via enhanced fire regime and degraded tortoise food base are, respectively, highly likely and likely to produce such effects.

Buffelgrass spread may interact with climate warming in additive or synergistic ways, such as by occupying high desert habitat and thus obstructing upward elevational shifts of tortoise populations in response to climate warming (D. Swann, pers. comm. 2014). In some areas, however, aridity may prevent buffelgrass from expanding under further climate warming and aridification, but unfortunately these are areas where climate effects alone are likely to threaten *G. morafkai* populations. Buffelgrass invasion is apparently by far the most severe effect of cattle ranching on *G. morafkai*, although under increasing climate stress it is possible that competition of tortoises and cattle for food could become apparent as an impact. The full impact of buffelgrass on tortoises is not yet evident, inasmuch as the limits to the spread of buffel have not been reached and are not yet known. Only limited attempts to control buffelgrass have as yet been made, and biological control has not been employed, and in these senses the inevitability of severe buffelgrass impacts may be questioned.

Anthropogenic climate warming looms as the greatest threat to desert tortoises and many other species of tortoises (Sinervo 2014) and other organisms, especially in the warmer regions of the planet. But here too there are significant uncertainties, both in the ultimate quantity and trajectory of warming that occurs over the coming 65-85 years and in the ability of desert tortoises, particularly *G. morafkai* for present purposes, to adjust. Given the generation time of chelonians and a rate of warming several-fold higher than during the past 3-65 million years (IPCC 2013; Diffenbaugh and Field 2013), evolutionary adaptation of tortoise physiology and behavior is a remote possibility.

Other compensatory responses to climate change are possible. Tortoises may change behavior in response to climatic stress and population declines; or, density-dependent factors may allow them to persist at lowered abundance despite climate impacts (see Discussion in Chapter 4). A widely expected response of organisms to climate warming, and in many cases to aridification, is distributional shifts northward and upward in elevation. Considering the phylogeny of turtles (Crawford et al. 2014; Guillon et al. 2012) and tortoises (Le, Raxworthy et al. 2006, Fritz and Bininda-Emonds 2007), and the geographic distribution of tortoise clades (van Dijk et al. 2014), the family shows very ancient patterns related to major plate tectonic land masses, and it is clear that tortoises are weak dispersers at large scales. Assumptions that tortoise populations can respond by range expansion should be regarded critically. For *G. morafkai*, there are likely at least two or three major obstacles to such compensatory distributional changes. This species is widely constrained from northward shift by relatively steep transitions from lower elevation subtropical and tropical environments to – in the United States – relatively cool temperate regimes above the sub-Mogollon mountains onto the elevated Colorado Plateau. Second, the montane elevational gradients up which *G. morafkai* would presumably migrate or expand are in many regions, especially in Mexico, along the scarp of the Sierra Madre Occidental, which rises steeply from tropical thornscrub to cooler woodlands and forests in most places. Warming that may impact tortoises might not be enough to make these geographically accessible environments suitable for a tortoise species whose normal activity in the Sonoran Desert region is primarily in hot weather and at body temperatures of 26-35 C. Recruitment in aridlands tortoise species is assumed to be climate sensitive, so under climatic stress expanding populations of young animals that are perhaps most likely to colonize newly suitable areas may be uncommon. Species may under climatic stress contract to core areas rather than expand at the edges (see Chapter 5) as we might hope.

While *G. morafkai* is currently thriving in some, possibly many localities in Mexico, we have identified serious threats that require further evaluation but are, in our estimation, likely to require large scale conservation efforts during coming decades. As these threats develop further, populations will contract and face genetic challenges associated with new environmental conditions in fragmented habitat, requiring novel legal and conservation biological efforts to prevent large-scale population extinctions.

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Chapter 2 Geographic Patterns of Mortality Observed in Desert Tortoises in Northwestern Mexico, 2001-2013

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ABSTRACT

We sampled populations of *Gopherus morafkai* (Morafka's, or Sonoran Desert tortoise) extensively during 2005-2013 throughout their Mexican distribution in Sonora and Sinaloa. Numerous carcass remains (N = 55) were found along with live tortoises (N = 291) over a wide area. A lower proportion of adults were found dead (11.3%) than subadults (19.3%) or juveniles (21.1%), but these were not statistically significant differences. We found statistically significant differences among biomes, with tropical deciduous forest (TDF) yielding lower proportions dead than thornscrub and deserts scrub. The highest proportion of carcasses in our samples were at low elevations in the most arid desert region we studied (50 % found dead) and in the hottest and driest region of thornscrub we sampled (36.5 % found dead). In the wettest and most well-shaded region we sampled, tropical deciduous forest in southern Sonora and northern Sinaloa, only 3.7 % of a large sample were found dead, and a smaller sample in the northern extension of thornscrub, with higher precipitation and lower temperatures, contained no mortalities, although data provided by other researchers included a low mortality fraction. Mortality overall was greater in areas at lower elevation and with lower precipitation and higher temperatures. Binomial regression showed that the elevation effect was subsumed by effects of precipitation and temperature, and that latitude (lower mortality further north) and biome (highest mortality in Sinaloan Thornscrub) were also important factors. We interpret these patterns as evidence of physiological stress in desert tortoises during at least 18 years of frequent drought and high temperatures, which is consistent with other data from a large part of the geographic distribution of *G. morafkai*.

2.1 INTRODUCTION

Throughout their range in the United States, desert tortoises (*Gopherus agassizii* in Mojave Desert and *G. morafkai* in Sonoran Desert) have suffered declines (Tracy et al. 2004; USFWS 2008, 2011; Chapter 5 in this report). *G. agassizii* was listed as federally threatened under the U.S. Endangered Species Act in 1990 as a result of declines and threats (USFWS 1990), and *G. morafkai* is currently being evaluated for similar listing (USFWS 2010, 2014). Mexico contains approximately 40 % of the range of *G. morafkai* as currently understood (southern populations in Mexico are genetically distinct and may belong to a separate taxon [Edwards et al. 2014, *submitted*]). As such, assigning protected status and designing conservation measures requires an understanding of population status and ecology of the species outside the United States. Although earlier reports (Averill-Murray et al. 2002) found that *G. morafkai*

populations were stable, data presented in Chapters 3-5 demonstrate that large mortality episodes associated with drought and, in several known cases, population declines have been widespread before and after 2000 in many parts of the species range in both countries. Here we describe geographic patterns of mortality observed as carcass remains in Mexico during extensive sampling 2005-2013. Our observations are related to climate in ways that suggest that regional drought and rising temperatures, which are projected to be further exacerbated by anthropogenic global climate change (Garfin et al. 2013), display patterns produced by climate-induced physiological stress.

2.2 METHODS

2.2.1 Fieldwork

Sampling was initiated with fieldwork led by Mercy Vaughn in the Comcáac lands (Seri Coast) of Sonora near Tiburon Island in 2001-2002. In 2005, we began a wider study in collaboration with Cristina Melendez of CEDES (Comisión de Ecología y Desarrollo Sustentable del Estado de Sonora), the state conservation authority of Sonora, to investigate various aspects of tortoise ecology in Mexico. We initiated fieldwork to collect samples for genetic analysis by Taylor Edwards and for health studies led by Dr. Mary Brown and Dr. Kristin Berry, and a telemetry-focused study on movements and coversite, microhabitat and habitat use was initiated in Alamos, Sonora, by Dr. Alice Karl. Dr. Karl further initiated a morphometrics study, with assistance from Dr. Philip Rosen, based on the initial observations in 2005. During 2005-2006 and 2008-2011, teams of volunteers were led by us in late summer and fall fieldwork. Continuous telemetry study was done 2005-2013 in Alamos. During summer and fall of 2012 and 2013, Dr. Rosen led transect-based fieldwork and initiated thermal ecology studies of desert tortoises in Sonora, working with a group of students and researchers from Mexico City and California. In fall, 2014, this work was expanded by Dr. Rafael Lara-Resendiz in Alamos and central Sonora. Sampling locations are shown in Fig. 2.1.

During 2005-2011, groups of experienced tortoise field biologists searched at random in the most auspicious-looking habitat, attempting to maximize the number of animals found. During 2012-2013 field biologists searched individually or in pairs searching separately along generally circular or oblong tracks recorded as digital tracks for calculating rate of occurrences. Digital data were stored in handheld Garmin global positioning system (GPS) units with accuracy ≈ 3 m, and recorded waypoints for all reptiles encountered during searches. Location of all tortoises, including carcass remains, were recorded as GPS waypoints, measurements (minimally midline carapace length [MCL], plastron length, mid-body carapace height, carapace width at two points, body mass) were taken, and sex was determined for individuals ≥ 180 mm MCL. Time and habitat for each tortoise were recorded. Numerous photographs were taken of most of the tortoises, including close-ups of the body and shell. During 2012-2013, and for some instances during 2005-2011, high resolution digital images were taken of carapacial scutes, with at least one portraying annular growth rings in the first lateral (costal) scute (which best displays growth rings as growth slows) and sometimes also the fourth lateral (which usually has less wear and clearer early rings than other scutes). Stage of decomposition and, where possible, size measurements (or size category) and sex were recorded for carcasses, and we attempted to identify injuries that may signify cause of death and the time since death, this was not done systematically. Nor were there any data on

decomposition rates in the more forested sites we studied, to assist in estimating time since death. Accordingly, time since death and cause of death are not presented here.

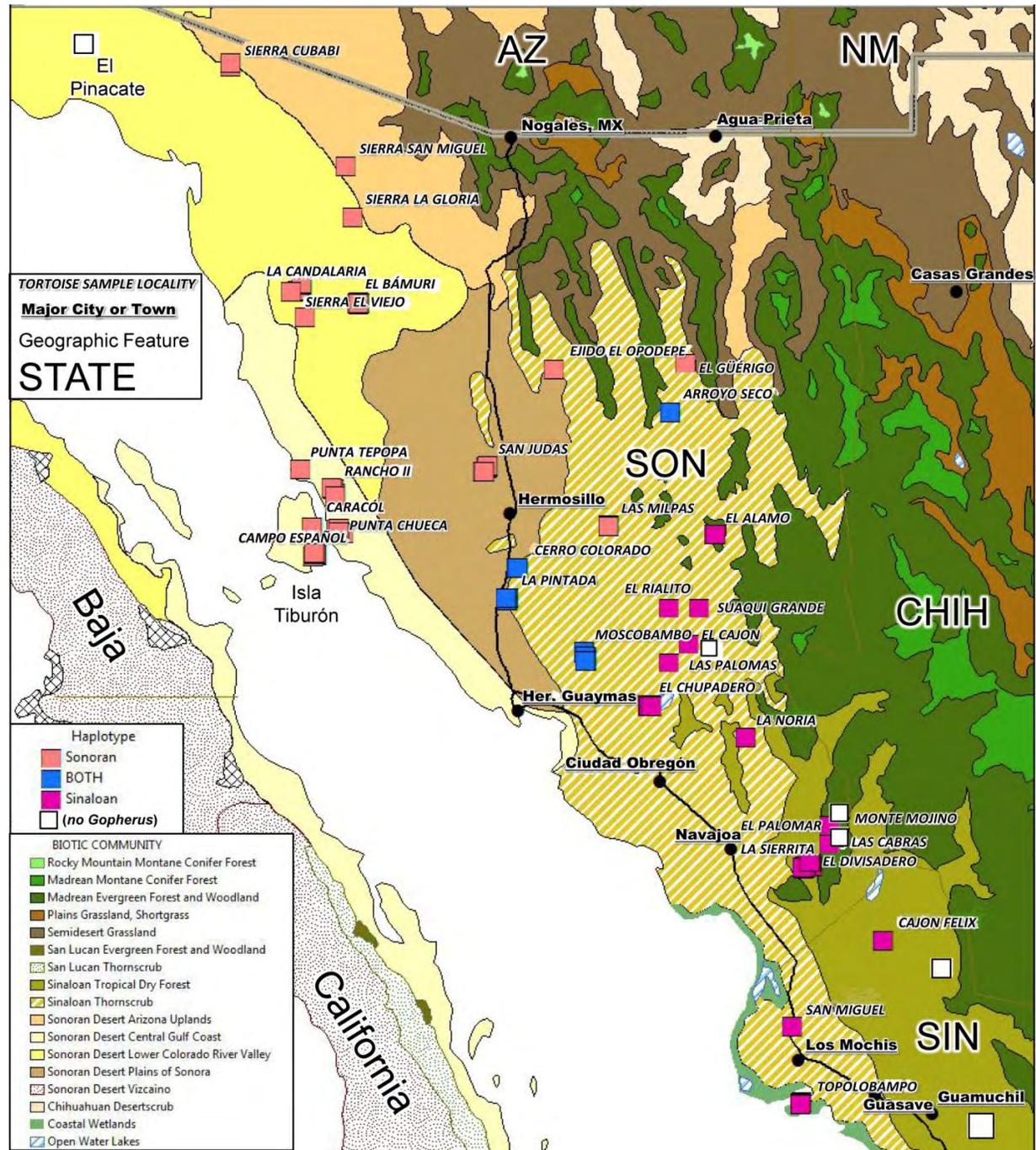


Figure 2.1. Sampling locations, biotic communities, and selected geographic sites referred to in this report.

2.2.2 Habitat Characterization

Desert tortoises in Mexico occur at elevations ranging from 5 – 1210 m in subtropical to tropical environments: Sonoran Desertscrub, Sinaloa thornscrub (most of which is in Sonora, not Sinaloa), and

tropical deciduous forest (TDF). Most (80%) of elevational records are between 123 and 606 m. We are aware of no records from semi-desert grassland or oak woodland, although *G. morafkai* exists in these higher elevation environments in the United States (Chapter 1). Thus, we categorized habitat according to the first three environmental types listed above, and further attempted to subdivide the gradation from short-stature tropical vegetation to relatively dense subtropical desertscrub, which is the gradient here termed thornscrub.

Thornscrub is a complex, tropical to subtropical vegetation community. It is dominated, on slopes, by broadleaf trees (often growing as large shrubs) with biogeographical affinities to TDF. The transition, going south, from Sonoran desertscrub to “Sinaloan” Thornscrub (which is Sinaloan in its affinity to TDF, although the great majority of it occurs in Sonora) is gradational and subject to interpretation (Brown 1980); as is the transition between thornscrub and tropical deciduous forest (TDF), which has been mapped in various ways. We evaluated available vegetation maps and GIS layers (Brown and Lowe 1980; INEGI 1996, 2005; Rzedowski 1978, 2006), recent literature and published maps on regional vegetation and floristics (Búrquez and Martínez- Yrizar 2010; Ceballos 2010; Felger et al. 2001, 2012), as well as our own observations of fauna and flora at our sample sites. The transition from Sonoran desertscrub to thornscrub mapped by Brown and Lowe (1980) is widely used and agreed with our field observations. We mapped the transition from thornscrub to TDF in Sonora by digitizing from published maps in Búrquez et al. (1999) and Felger et al. (2012), which correctly represented changes in vegetation structure and flora we found during tortoise sampling. Our concept of the variation in thornscrub follows INEGI (2000), in which thornscrub dominated by microphyllous trees, shrubs, and with open ground and ephemeral forbs can be categorized as desert-like, while environments with many broadleaf deciduous trees or large shrubs with closed canopy on slopes may be categorized as TDF-like. In this construct, Sinaloan Thornscrub varies significantly from a relatively mesic to a relatively more arid presentation, and TDF extend north to San Xavier in central Sonora and to near the Rio Yaqui northwest of Bacanora, only 230 km south of the U.S.-Mexico border.

2.2.3 Climatic Variables and Elevation

Climatic data were obtained from the National Climate Information Center, WorldClim Global Climate Data, Prism Climate Group, National Atmospheric and Oceanic Administration, and published literature. We used two WorldClim GIS raster layers for bioclimate (Bioclim1 [mean annual precipitation]; Bioclim12 [mean annual temperature]) and extracted the raster values to the point data we obtained for live and dead desert tortoises using the extract-to-points spatial analyst tool in ArcGIS 10. We verified these values by checking against annual means for nearby weather stations. Elevation was taken from GPS readings, when available, or, if not, from Google Earth maps on which the tortoise observation points were projected.

2.2.4 Analysis

We summarized data as mortality fractions (the percentage or proportion of a total sample composed of animals found dead) and performed simple statistics (*t*-tests, chi-square tests) and graphics in Microsoft Excel. We then uploaded the dataset into SAS JMP and performed binomial regression models judged by AICc on the odds of *LIVE* versus *DEAD*. We entered each of the following variables singly and in combination: LATITUDE (decimal degrees), ELEVATION (m), PRECIPITATION (mean annual, mm),

TEMPERATURE (mean annual, degrees C), BIOME (Sonoran Desertscrub, Sinaloa Thornscrub, Tropical Deciduous Forest), and BIOTIC COMMUNITY (Lower Colorado River Valley, Arizona Upland, Plains of Sonora, Sinaloa Thornscrub, and Tropical Deciduous Forest).

2.3 RESULTS

We found 56 dead tortoises in a total sample of 338 field-observed individuals (16.6% of the sample) of *G. morafkai* in northwestern Mexico during 2005-2013 (Table 2.1). The mortality percentage was lowest in adults and highest in juveniles and subadults, but the differences are not statistically significant (Fisher's exact test, $P \geq 0.061$).

Table 2.1. Mortality of three age classes of desert tortoises found during field surveys in northwestern Mexico, 2005-2013.

Age Class	DEAD	LIVE	% Dead	N
Adult (≥ 210 mm MCL)	30	234	11.4%	264
Subadult	4	18	18.2%	22
Juvenile (< 180 mm MCL)	8	30	21.1%	38
undetermined	14	0		14
TOTAL	56	282	16.6%	338

Percentages of mortality were low in TDF and the northeasterly thornscrub region in north-central Sonora, as well as among small samples from Arizona Upland and Plains of Sonora Sonoran Desertscrub north of Caborca and Hermosillo, respectively (Fig. 2.2, Table 2.2). Overall, observed mortality fraction in TDF was significantly lower than in either desertscrub or thornscrub (Fisher's exact tests, $P < 0.00001$), whereas desertscrub and thornscrub fractions were not ($P = 0.16$, 2-tailed). By contrast, on and near Isla Tiburón and the nearby coastal mainland (the "Seri Coast" region of the Central Gulf Coast Sonoran Desertscrub), 50% of 40 individuals were found dead. Relatively high mortality percentage was also found in the thornscrub lowlands, in coastal Sinaloa and south-central Sonora: 36.5% of 52 individuals recorded were found dead. These two high mortality fractions were not significantly different from each other (Fisher's exact test, $P = 0.29$) but were each significantly higher than all other sites combined ($P < 0.005$) and when combined, were significantly higher than any site with $N \geq 6$ (see Fig. 2.2; Fisher's exact tests, all $P < 0.04$). This represents a high-mortality region at low elevation, extending southeast from Central Gulf Coastal Sonoran Desertscrub through Sinaloa Thornscrub, possibly extending into Coastal Thornscrub at Topolobampo, Sinaloa.

Within-biotic community values comparing elevation and climatic variables for live and dead tortoise records are in Table 2.3. In the overall ample and specifically within Sinaloa Thornscrub, dead tortoises were found at localities with significantly lower mean annual precipitation and higher mean annual temperature, and at lower elevation than live tortoises. In Lower Colorado Valley Sonoran Desertscrub, differences were in the opposite direction for precipitation and elevation, although the differences were small in absolute terms.

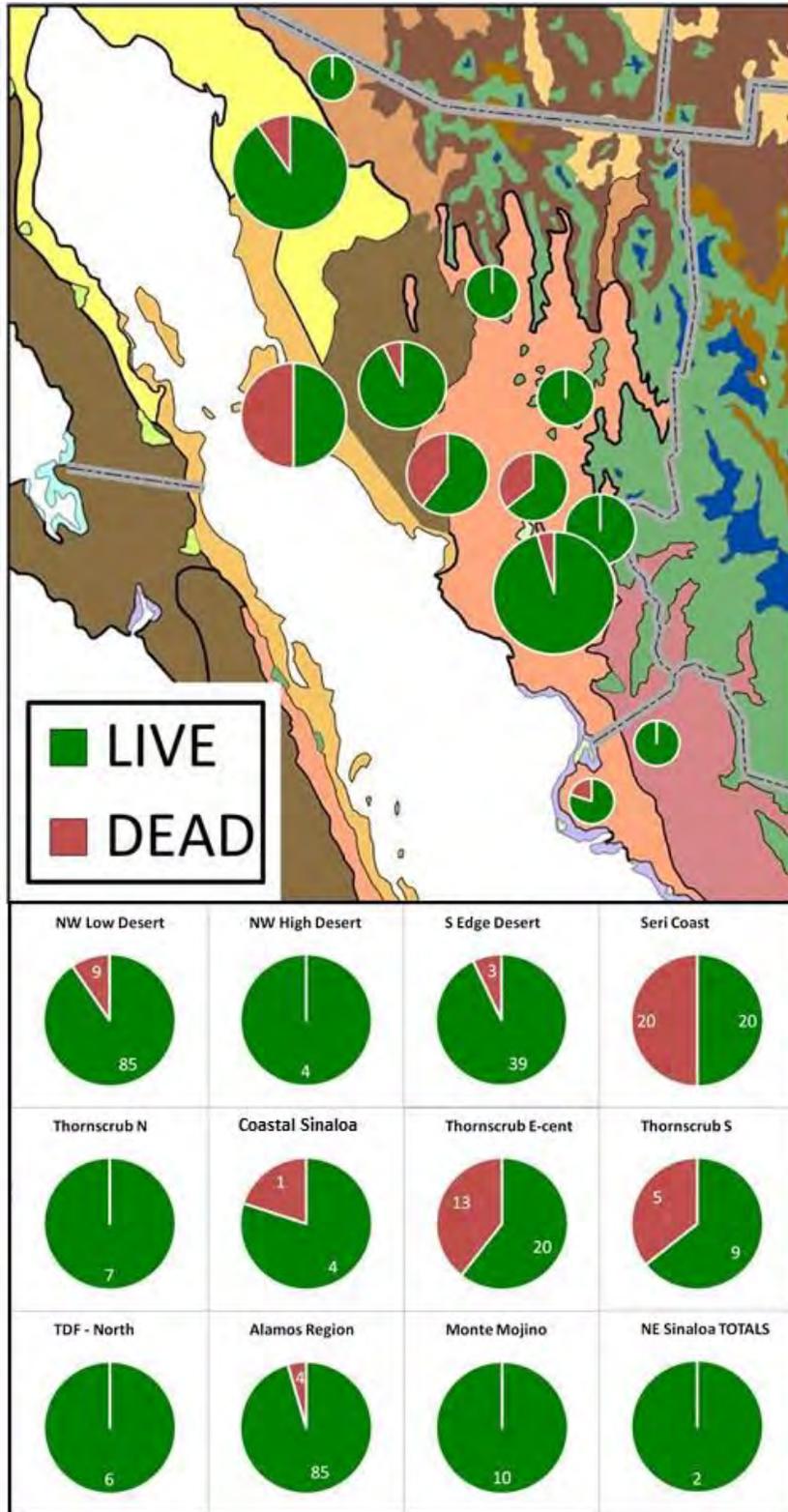


Figure 2.2. Distribution of mortality fractions observed in samples of *Gopherus morafkai* in northwestern Mexico 2005-2013. Circle sizes on map are relative to sample sizes (pie charts below the map). Biotic community types are as in Fig 1. Seri Coast refers to part of the Central Gulf Coast where we sampled, on and near Isla Tiburón.

Table 2.2. Elevation, climate variables, and dead and live desert tortoises, shown according to biotic communities and sampling localities, based on WorldClim data and surveys in northwestern Mexico, 2005-2013.

Biotic Community, Locality Name	Elevation (m)	Annual Precip (mm)	mean Annual Temp (C)	% DEAD	No. Found DEAD	No. Found Live	N
Arizona Upland	624	273	19.9	0.0%	0	4	4
Sierra Cubabi	553	239	20.3	0.0%		2	2
Sierra La Gloria	491	266	20.3	0.0%		1	1
Sierra San Manuel	899	349	18.6	0.0%		1	1
Central Gulf Coast	138	138	22.6	50.0%	20	20	40
Campo Español	69	122	22.8	75.0%	9	3	12
Caracól	207	143	22.1	25.0%	1	3	4
Punta Chueca	105	136	22.9	30.8%	4	9	13
Punta Chueca E	84	134	23.0	0.0%		3	3
Punto Tepopa	148	136	22.0	100.0%	1		1
Rancho II	302	167	21.8	71.4%	5	2	7
Lower Colorado Valley	375	196	20.5	9.6%	9	85	94
El Bámuri	448	254	20.3	35.7%	5	9	14
La Candelaria	333	185	20.6	0.0%		20	20
Sierra El Viejo	372	187	20.5	6.7%	4	56	60
Plains of Sonora	308	323	23.4	9.4%	3	29	32
Cerro Colorado	311	337	23.8	10.0%	1	9	10
La Pintada	241	318	23.8	7.7%	1	12	13
San Judas	400	315	22.4	11.1%	1	8	9
Sonoran Desert (overall)	313	208	21.5	18.8%	32	138	170
Tropical Deciduous Forest	418	685	23.2	5.1%	5	94	99
Cajon Felix	213	732	24.4	0.0%		2	2
El Alamo	796	597	21.7	0.0%		4	4
El Divisadero	327	653	23.8	0.0%		11	11
El Palomar	484	687	23.2	0.0%		15	15
La Majarra	339	681	23.9	0.0%		2	2
La Noria	433	704	23.3	0.0%		2	2
La Sierrita	456	701	22.7	6.9%	2	27	29
Las Cabras	344	670	23.5	11.5%	3	23	26
Monte Mojino	399	740	23.3	0.0%		8	8
Sinaloan Thornscrub	350	431	23.8	27.5%	19	50	69
Arroyo Seco	1011	518	20.2	0.0%		3	3
Ejido El Opodepe	704	471	20.7	0.0%		1	1
El Chupadero	245	440	24.5	22.2%	4	14	18
El Güérigo	1125	551	19.0	0.0%		3	3
Las Milpas	527	454	23.4	0.0%		10	10
Moscobampo	231	372	24.3	60.0%	9	6	15
San Miguel	132	462	23.5	0.0%		1	1
Suaqui Grande	270	469	24.4	35.7%	5	9	14
Topolobampo	58	281	24.6	25.0%	1	3	4
overall means	351	393	22.5	16.6%	56	282	338

Table 2.3. Comparison of mean annual precipitation, mean annual temperature, and elevation for desert tortoise found live versus dead in six biotic communities during surveys in northwestern Mexico, 2005-2013. Means and standard errors are shown for live and dead tortoises for the three variables. Asterisks indicate significantly different values for live and dead tortoises based on *t*-tests ($P < 0.05$).

	Arizona Upland	Central Gulf Coast	Lower Colorado Valley	Plains of Sonora	Sinaloan Thornscrub	Tropical Deciduous Forest	ALL
Annual Precip (mm)							
DEAD		139.6 ± 4.2	218.2 ± 9.6 *	317.0 ± 9.0	411.7 ± 13.2 *	677.2 ± 8.2	302.0 ± 22.8 *
LIVE	273.3 ± 26.7	136.0 ± 3.1	193.9 ± 2.7	323.5 ± 2.0	441.4 ± 8.5	685.0 ± 3.3	411.8 ± 12.9
both	273.3 ± 26.7	137.8 ± 2.6	196.2 ± 2.7	322.9 ± 2.0	433.2 ± 7.3	684.6 ± 3.1	393.6 ± 11.6
mean Annual Temp (C)							
DEAD		22.4 ± 0.10 *	20.4 ± 0.07	23.5 ± 0.44	24.4 ± 0.05 *	23.3 ± 0.20	22.9 ± 0.19 *
LIVE	19.9 ± 0.44	22.8 ± 0.11	20.5 ± 0.02	23.4 ± 0.12	23.6 ± 0.23	23.2 ± 0.06	22.4 ± 0.09
both	19.9 ± 0.44	22.6 ± 0.08	20.5 ± 0.02	23.4 ± 0.12	23.8 ± 0.17	23.2 ± 0.06	22.5 ± 0.08
Elevation (m)							
DEAD		157.7 ± 21.5	403.9 ± 17.8 *	106.2 ± 106.2	236.9 ± 13.4 *	108.5 ± 108.5	217.0 ± 18.5 *
LIVE	623.6 ± 93.0	119.1 ± 20.0	372.1 ± 6.1	328.4 ± 15.3	400.3 ± 41.2	434.3 ± 16.5	379.0 ± 10.8
both	623.6 ± 93.0	138.4 ± 14.8	375.1 ± 5.8	307.6 ± 19.9	355.3 ± 31.2	417.9 ± 17.9	352.1 ± 10.0

Binomial regression predicting life status (live or dead) was significant for latitude, elevation, precipitation, temperature, and biome, but the univariate relationship was strongest for elevation. However, in combinations using precipitation, temperature, and elevation, the latter was always excluded as an inferior predictor. The best binomial model, with generalized $R^2 = 0.30$, $AICc = 249.28$, $\Delta AICc > 2$, $P < 0.001$ for latitude and precipitation, and $P < 0.05$ for temperature and biome, was: $\text{odds(LIVE)} = \text{int} + (0.0103 * \text{PRECIP}[\text{mm}] + 0.168 * \text{LATITUDE}[\text{degN}] - 0.346 * \text{TEMPERATURE}[\text{degC}]) * \text{BIOME}$. In this model, Sinaloan Thornscrub was a significant factor in predicting higher mortality. No crossed effects were significant or included in any model combination with low AICc.

2.4 DISCUSSION

Results of this study demonstrate that mortality of *Gopherus morafkai* observed as carcasses during tortoise sampling (2005-2013) in northwestern Mexico varied geographically and with biotic community. It was significantly associated positively with temperature and negatively with elevation and precipitation and variables presented in Table 2.2. High mortality samples occurred together in a zone extending from the central gulf coast southeast into low-elevation thornscrub, and possibly extending southward in Coastal Thornscrub in northern Sinaloa. Binomial regression models indicated that the elevational effect was dependent on co-variation with precipitation and temperature, and also showed that mortality was negatively correlated with latitude. In other words, observed mortality of desert tortoises in Mexico was greater in dry, hot, low elevation sites and further south. These findings signal that climate stress (heat and drought) may be contributing substantially to mortality, in some cases quite high mortality. Specifically, observed mortality was highest in a region extending from central gulf coastal Sonora (50% of sample found dead), southward into low-elevation thornscrub in south-central Sonora, and possibly further south into Sinaloa in low-elevation thornscrub (36.5% of the sample found dead). These sample fraction values that signaled population declines at *G. morafkai* census plots in Arizona (Chapter 5).

Although Sinaloan Thornscrub is generally significantly wetter, more tropical, and shadier than desertscrub, mortality varied within the thornscrub region. Mortality in thornscrub was lower in the north and at higher elevation. Mortality in thornscrub was high at sites at lower elevations (58-270 m versus 527-1125 m), at hotter sites (23.5-24.6 versus 19.0-23.4 C mean annual temperature), and drier sites (281-469 versus 454-551 mm mean annual precipitation). Precipitation in drier parts of the thornscrub is equal to or less than that in Arizona Upland sites in the United States where drought-related die-offs and population declines have been observed. Thus, it is possible that episodic drought, rather than high temperatures acting directly on tortoise homeostasis, may be responsible for the observed high mortality regions in northwestern Mexico.

The central gulf coast mortality occurred in the most arid region we sampled, at a series of low-elevation sites, some of which also had mass mortality with evidence of population declines in the late 1990s and early 2000s (Vaughn et al., Chapter 3), suggesting that this drought-related



Figure 2.3. Shell of freshly killed immature desert tortoise in tropical deciduous forest in Alamos, Sonora, October 2012. The intact find (left) illustrates the difficulty of observing such remains on the leaf litter. Indications of predation by a large mammal are visible at right.



Figure 2.4. Remains of a desert tortoise at a cave entrance in thornscrub at Moscobampo in central Sonora, presumed to have been killed by a mountain lion.

die-off may be long in duration or recurring. The thornscrub mortality was in a region with higher precipitation but also the highest temperatures in the region. It is not clear whether drought or high temperatures, or both, are involved in the observed high mortality. Although Sinaloan Thornscrub is generally significantly wetter,

more tropical, and shadier than desertscrub, mortality varied within the thornscrub region. Mortality in thornscrub was lower in the north and at higher elevation: it was higher at sites at lower elevations (58-270 m versus 527-1125 m), at hotter sites (23.5-24.6 versus 19.0-23.4 C mean annual temperature), and drier sites (281-469 versus 454-551 mm mean annual precipitation). Precipitation in drier parts of the thornscrub is equal to or less than that in Arizona Upland sites in the United States where drought-related die-offs and population declines have been observed. Thus, it is possible that episodic drought, rather than high temperatures acting directly on tortoise homeostasis, may be responsible for the observed high mortality regions in northwestern Mexico.

One seemingly anomalous result was an association of mortality with greater elevation and precipitation in our samples from the relatively arid Lower Colorado River Valley Sonoran Desertscrub in northwestern Sonora. Although we found dead tortoises in several places, they were disproportionately in canyon mouths and on a ranch at higher elevation. The core of the population we studied was in a mid-valley wash and adjoining bajadas, where productivity was high despite the low elevation (see Chapter 7) and mortality was low. Thus, the unexpected differences in this biotic community probably reflect local variation associated with shelter quality, habitat productivity, and ultimately soil moisture availability.

Other field studies have reported mortality fractions similar to the overall rate of 16.6% we recorded in 2005-2013. Treviño et al. (1992) at six localities in the Hermosillo region in 1990 reported 2 dead and 14 live tortoises on transects (12.5% mortality fraction). Field notes (Fritts 1983) and museum specimens resulting from Fritts and Jennings's (1994) survey of tortoises in northwestern Mexico include 5 dead (four from northern thornscrub, one from TDF near El Fuerte, Sinaloa) and 19 live (21 % mortality fraction). Field biologists participating in the Madrean Archipelago Biodiversity Assessment found 1 dead and 10 live tortoises (9 % mortality fraction) in the northern thornscrub (in addition, they found three live and two dead on roads and one killed by a person near a large dam). We recognize that there may be sampling artifacts associated with some of these surveys, but data were collected consistently by field biologists. Fritts and Jennings (1994; Fritts 1983, field notes) also recorded at least 12 records of tortoise carcasses shown or given to them by local people, most or all having been used as food. In contrast, we found only limited evidence that people were still using tortoises as food (Chapter 1).

We did not identify the cause of most of the mortality we recorded. We suspect that desert tortoise mortality is more likely to be associated with drought in more arid regions of northwestern Mexico, as indicated by Karl (2004) for Mojave Desert and demonstrated by Zylstra et al. (2012) for Sonoran Desert Arizona. In tropical deciduous forest, predators may have an influence that is generally absent in the desert. High predator diversity includes at least three cats (jaguar, ocelot, and margay) that are absent in the desert, although both jaguars and ocelots are notably present in thornscrub near Sahuaripa at the north margin of the forest. Predation by large felids may be less likely to leave a conspicuous long-

lasting tortoise shell (Figs. 3 and 4), especially in forest habitat. We suspect this partially accounts for the very low mortality fraction we found in TDF. In the years we worked in that environment they were so rarely found ($n = 3$) that we think that rapid decomposition cannot solely explain our finding. Intact carcasses last several years in TDF (M. Figueroa, pers. comm., 2014). We suggest that predation mortality is higher in TDF than elsewhere, with predators crushing or removing carcasses to feeding stations (Fig. 2.3), or total mortality is lower in TDF. Possibly, carcasses are more difficult to find in the denser litter and brush, as well. In any case, decomposition rate differences among our sampling stations cannot account for the very high mortality in particularly hot, arid sections of the Sonoran Desert and Sinaloan Thornscrub in Mexico.

We found that mean age (determined by growth rings, assuming one ring per year) of adult-sized desert tortoises ($MCL \geq 210$ mm) in thornscrub was lower than that in TDF or desertscrub in Mexico (Chapter 7), which is consistent with the high mortality found in a large part of the thornscrub. The difference occurred in younger age classes (< 20 yr), which we attributed to higher juvenile survivorship or reproductive success (or both) in relatively mesic forest habitat (Chapter 7). However, age structure in all three biomes in Mexico showed a remarkable scarcity of animals over 30 years of age or with the worn annuli seen in very old adult desert tortoises. We suspect that relaxation of human predation on tortoises over the last 1-3 decades may help explain this, with the strongest decrease in Alamos region TDF, where we sampled most intensively and were most consistently told that people no longer use tortoises as food (Chapter 1).

The best way to explain the available data is that in recent years, 1995-2013, characterized overall by several drought periods and elevated temperatures, desert tortoises in parts of the Sonoran Desert and Sinaloan Thornscrub in Mexico have experienced high mortality. By contrast, in the TDF abundance appears to be relatively high (Chapter 7), and demographic parameters indicate strong populations in a wetter climate further ameliorated by forest shade and reduced human predation.

ACKNOWLEDGEMENTS

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Chapter 3 Desert Tortoise (*Gopherus morafkai*) Mortality Surveys and Paraecology Training on Comcáac (Seri) Lands, Coastal Sonora, Mexico

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ABSTRACT

Gopherus morafkai (Morafka's or Sonoran Desert tortoise) is culturally significant to the Comcáac (Seri Indians) of Sonora, Mexico. In response to reports by the Comcáac of high desert tortoise mortality on Isla Tiburón, a protected area of their territory Gulf of California, we conducted tortoise mortality plot surveys at one island site in October 2001 and two mainland sites in October 2002 within Comcáac territory. Researchers trained a team of Comcáac field workers to conduct tortoise surveys and handle tortoises according to protocols developed in the United States. We observed high and recent mortality at all three plot sites, and Comcáac observers reported similar mortality at a fourth site that we did not survey. These findings are similar to mortality episodes observed at several sites in Arizona, and as in Arizona are correlated with drought, indicating that die-offs and population reductions are occurring widely throughout the species' distribution.

3.1 INTRODUCTION

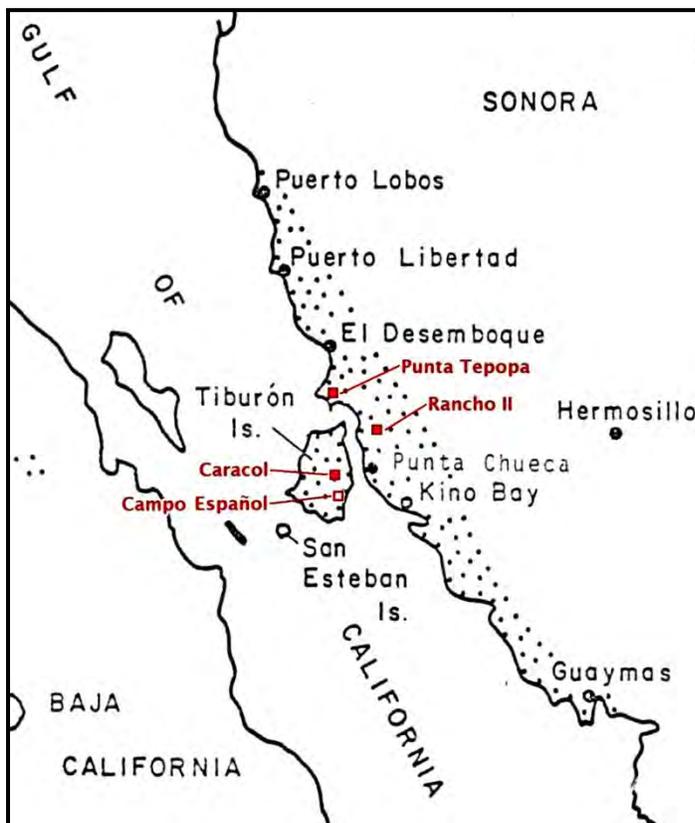
The Comcáac (Seri Indians) are a small fishing-based community on the coast of the Gulf of California in Sonora, Mexico. The desert tortoise and its habits are the subject of many songs and stories within the Comcáac culture (Felger et al. 1981, Nabhan 2002). The archaic Comcáac name for the desert tortoise is *xtamoosni*. The name comes from the root *moosni*, which is the generic name for turtles and tortoises, including the sea turtle *Chelonia mydas*. The prefix "xta-" implies "of the land." Nicknames now commonly used for the desert tortoise are: *ziix hehet cōqijj* ("thing that sits among plants") and *ziix catotim* ("thing that slowly scoots along"). These names and words for ecological terms (e.g., words for burrow, plastron, carapace, and hibernation) show the extent of traditional ecological knowledge found in the modern culture and language (Nabhan 2002).

Prior to 2001, people reported to Gary Paul Nabhan (pers. comm., 2001) that they noticed many tortoise remains on Tiburón Island as they were surveying and hunting for desert bighorn. This and the cultural importance of the species motivated us to include it in a paraecology training program conducted by the Center for Sustainable Environments at Northern Arizona University. We trained a team of Comcáac field researchers in tortoise survey and handling techniques similar to those used in the United States. In October 2001, American researchers and Comcáac who participated in the original surveys with Osorio

and Bury (1982) collaborated on a desert tortoise mortality survey on Tiburón Island, and in October 2002 we expanded the study to include adjacent mainland coastal areas in Comcáac territory.

Throughout their range in the United States, desert tortoises (*G. agassizii* in Mojave Desert and *G. morafkai* in Sonoran Desert) have suffered declines (USFWS 2011; see Chapter 5 in this report). Mexico contains approximately 40% of the range of *G. morafkai* (Auffenberg 1978) as currently understood (southern populations in Mexico are genetically distinct and may belong to a separate taxon [Edwards et al. 2014, submitted]), and thus understanding population status and ecology of the species outside the United States is relevant to current consideration for listing the species as threatened under the U.S. Endangered Species Act (USFWS 2010). Although earlier reports (Arizona Interagency Desert Tortoise Team 2000; Averill-Murray et al. 2001, 2002) found that *G. morafkai* populations were stable, the data herein and in Chapters 2, 4, and 5 demonstrate that large mortality episodes associated with drought and, in several known cases, population declines, have been widespread before and after 2000 in many parts of the species range in both countries.

3.2 METHODS



Paraecology training involved providing the Comcáac field workers, who were bi-lingual, with Spanish translations of desert tortoise survey and handling protocols in use in Mojave Desert, including live capture form, health profile form and a shell-skeletal remains form. We also provided a shell wear class key and a brief on natural history of the desert tortoise. Comcáac participants were self-selected, and some had participated in other U.S.-led tortoise studies on their territory (Reyes Osorio and Bury 1982). We trained 14 paraecology

Figure 3.1. Study sites established in Comcáac (Seri Indian) territory (stippled) in central gulf coastal Sonora, Mexico in 2001 and 2002.

students to set up study plots, fill out survey forms, and process live tortoises and shell-skeletal remains. Although traditional ecological knowledge was not the primary focus of our work, we report important information that was transmitted to us by elders at separate training sessions.

We report observations from four sites established within current Comcáac territory (Fig. 3.1), which is in central coastal Sonora from just south of the village of Punta Chueca to north of Desemboque and

includes Isla Tiburón Island. Tiburón has been a protected site since 1963. It has a large herd of bighorn sheep (*Ovis conadensis*) but no livestock grazing. Both the island and mainland areas are in the Central Gulf Coast phytogeographic province of the Sonoran Desert, which is a low-elevation, arid region characterized by shrubs, small desert trees (or “shrub-trees”), cacti, sandy soils, and extensive areas of low granitic mountains (Felger and Wilder 2013).

In October 2001, we established a survey plot site at Caracól, near a field station on Isla Tiburón. In October 2002, we established study sites at Rancho II and Punta Tepopa on the coastal mainland. The Caracól site is located near the central portion of Isla Tiburón, 4.8 km from the eastern shore. Elevation on the site ranges from 100-300 m. The Rancho II site was established 18 km north of the Comcáac village of Punta Chueca and 4.5 km east of the Sea of Cortez 250- 450 m elevation. The Punta Tepopa site is located on the south side of the isolated mountain range on the Tepopa peninsula with an elevation range of 100-200 m and 2.5 km from the Sea of Cortez. We established the Campo Español site near the eastern shore on the southern portion of the island at 100-200 m elevation and 1.5 km from the Canal de Infernillo.

The Punta Tepopa plot is 0.5 km² while the others are 1 km² in size. We set up 100 x 100 m grid cells using handheld GPS units, marked with rebar sheathed by 10 ft PVC at each grid cell corner. We conducted a single coverage on each plot by walking 10 m wide transects. All researchers gathered to process all live and dead tortoises encountered using the data sheets in Appendices A-C. The fourth site, Campo Español, was observed by Comcáac participants but not formally surveyed. Reyes Osorio and Bury (1982) also surveyed tortoises at Caracól, although we did not relocate their exact study transects, and they reported on transect surveys at five additional plots on Tiburón south of Caracól, including at Valle de los Españoles near our fourth site.

Climatic data for the nearest site with long-term data, Hermosillo, Sonora, were obtained from WorldClim Global Climate Data and Prism Climate Group. For missing temperature values in October-December 2002, we used monthly means computed for 1966-2004.

3.3 RESULTS

3.3.1 Mortality

On Isla Tiburón Island in 2001 we found 30 dead and 10 live tortoises on the Caracól plot (75 % dead). On the mainland in 2002 we found 13 dead and 9 live tortoises on the Rancho II plot (58 % dead) and 6 dead and 10 live tortoises (38 % dead) on the Punta Tepopa plot (Fig. 3.2). We might have found more remains at Punta Tepopa, but many may have been washed downslope and buried prior to our survey.

Although we did not survey the Campo Español site, the Comcáac stockpiled shell-skeletal remains of over 25 tortoises in a wash prior to our arrival. They collected these approximately 1 km east of the plot earlier in 2001. In October of 2001 a tropical storm washed most of the remains down the wash and out to sea.

Estimated time since death for most of the tortoise shell-skeletal remains found at the three study sites was less than four years (Fig. 3.3). Of 49 remains found on the three plots, 42 were from animals that

had died within four years prior to our surveys (Table 3.1). At Caracól, 29 of 30 remains were from animals that died within four years of our survey, as were 11 of 13 at Rancho II and 2 of 6 at Punta Tepopa.

Table 3.1. Estimated years of mortality for carcass remains of *Gopherus morafkai* found in at study plots in 2001 on Isla Tiburón (Caracól) and in 2002 on adjoining coastal mainland, Sonora, Mexico.

	2001	2000-2001	1999-2000	1997-1999	before 1997
Caracól	0	1	10	18	1
	2002	2001-2002	2000-2001	1998-2000	before 1998
Rancho II	1	6	1	3	2
Punta Tepopa	0	0	1	1	4

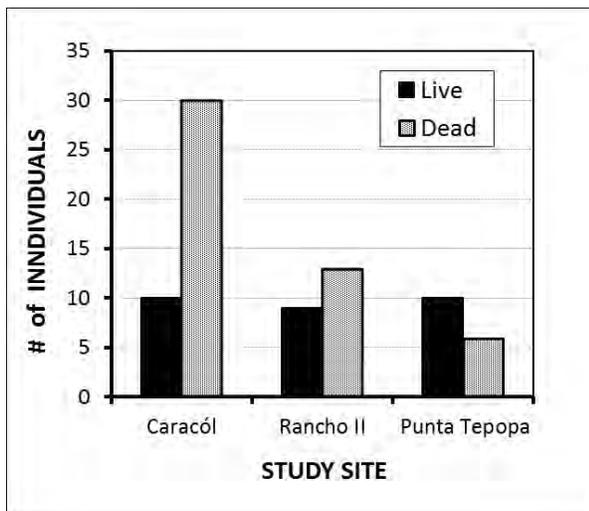


Figure 3.2. *Gopherus morafkai* observed on study plots on Isla Tiburón (Caracól) and the adjoining coastal mainland in 2001 and 2002.

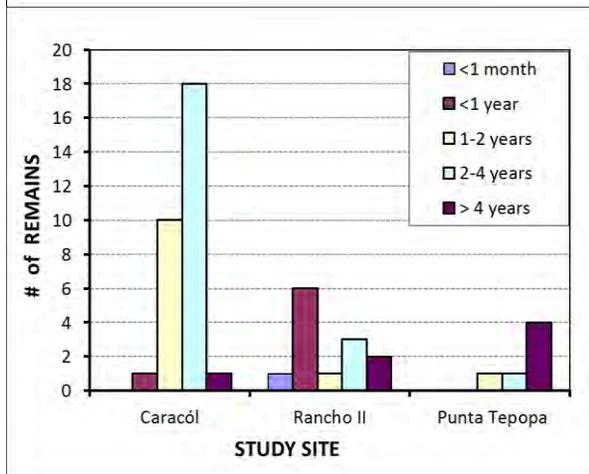


Figure 3.3. Estimated time since death for *Gopherus morafkai* carcasses found in 2001 on Isla Tiburón (Caracól) and the adjoining coastal mainland in 2002.

3.3.2 Climatic History

Rainfall and temperature history at Hermosillo, 120 km east of our study areas, during and prior to our surveys are shown in Fig. 3.4, and generalized patterns for parts of Sonora (Hallack-Alegria and Watkins 2007), that likely shared climate fluxes with our study areas are shown in

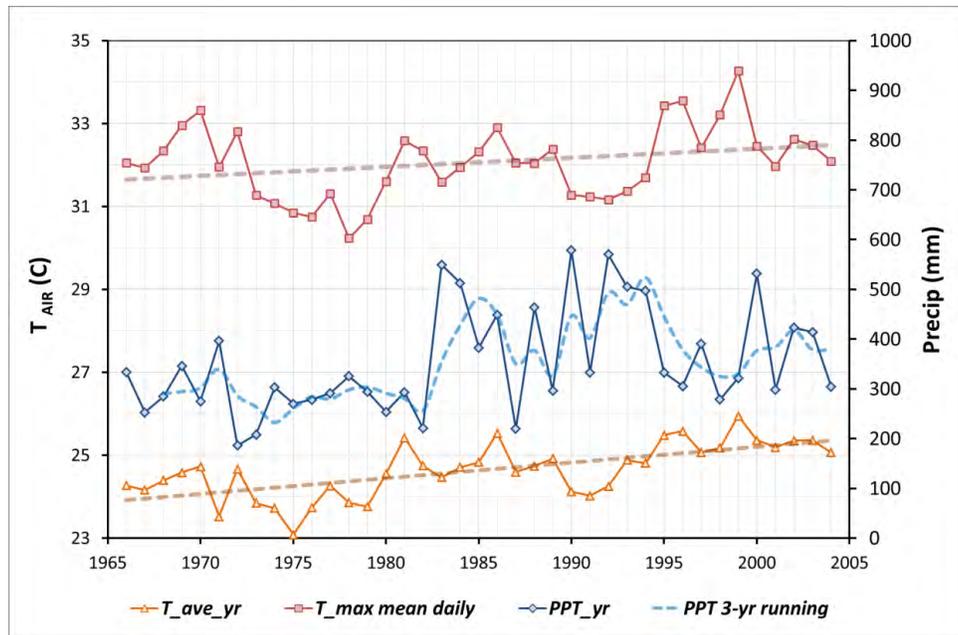


Figure 3.4. Temperature and precipitation record from Hermosillo, Sonora, Mexico 1966-2004. Missing temperature data for October-December 2002 were adjusted to monthly means for the period.

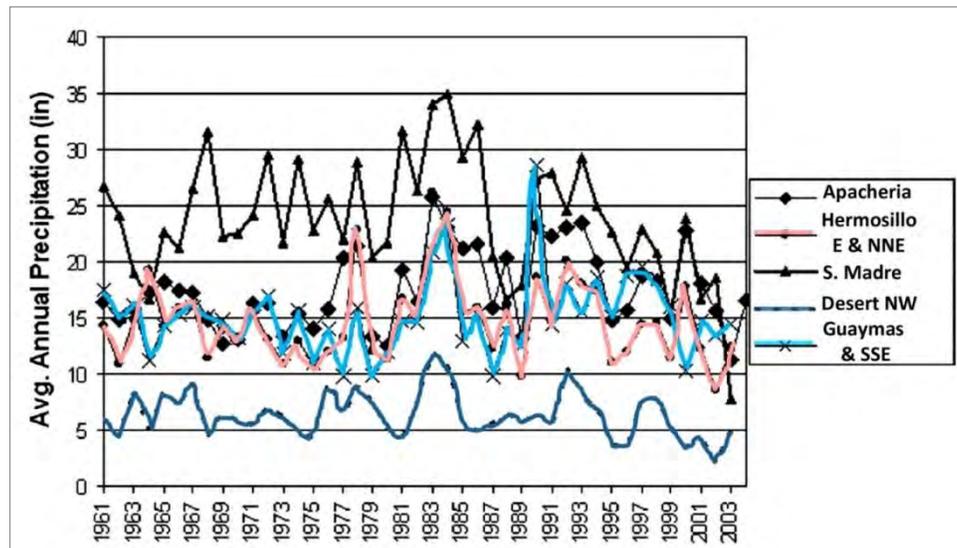


Figure 3.5. Precipitation history in the Sonora, Mexico region, modified from Hallack-Alegria and Watkins (2007).

Fig. 3.5. Rainfall and temperature fluctuated throughout these records. Recorded rainfall was lower during 1961-1982 than during 1983-1994, but drier times returned during 1995-2005 with some areas showing severe drought in 2002. These trends are similar to those seen in Arizona (Chapters 4 and 5).

Temperatures showed upward trends, with 1995-1996 and 1998-1999 representing a very warm period, as seen elsewhere in the region (Garfin et al. 2013).

3.3.3 Live Tortoise Sex Ratios and Health Status

At Caracól we found seven females, two males and one immature tortoise. At Rancho II we found four females, four males, and one immature tortoise. At Punta Tepopa, we found ten adult females, eight of which were inside a single rock shelter.

On the Punta Tepopa study plot, six of the ten tortoises we found showed evidence of upper respiratory tract disease (URTD). Symptoms exhibited included swollen eyes and a dried, white crust around the mouth, severe head swelling restricting ability to fully open eyes, swelling of the lower palpebra, and ocular and nasal discharge. Of the eight communally denning females, five showed signs of disease. We saw no apparent evidence of URTD in the live tortoises on the Isla Tiburón or Rancho II study plots, but we observed one adult tortoise with green nasal exudate on the road to Rancho II approximately 1 km west of the plot. We observed no evidence of shell disease on any of the tortoises on either the island or the mainland.

3.4 DISCUSSION

More than a third of *Gopherus morafkai*'s geographic distribution lies south of the U.S.-Mexico border in northwestern Mexico. Aside from general distribution and basic ecology there is limited knowledge on the status of the populations in Mexico. The 2001-2002 surveys reported here are the first repeat-monitoring conducted on the current status of desert tortoises in Mexico. The mortality rates we observed (38 – 75 % of samples found dead) are very high and are similar to the values in Arizona populations that were associated with and likely signify large population reductions (Chapter 5). The Comcáac have reported a recent die-off of equal severity throughout Tiburón Island where tortoises occur. Thus, a widespread mortality episode was underway in this region of central gulf coastal Sonora during or just before our surveys.

The rates of encounter of live tortoise in our surveys were 9-12 (mean 10.33) per km², which is 15.9 % of the 28.9 – 87.3 (mean 65) per km² reported by Reyes Osorio and Bury (1982) using comparable methods on Isla Tiburón in 1978-1979. During the 1978-1979 surveys, 2 dead and 10 live tortoises were reported from near Caracól (16% dead) and an additional 136 live tortoises were reported from other transects on the island (although Osorio and Bury do not mention dead tortoises in these additional surveys, they presumably would have reported heavy mortality had it been evident). Regardless, the comparison with the data from 1978-1979 demonstrates that the die-off we observed two decades later was not occurring then. Further, these data indicate that tortoise abundances in the study region apparently declined sharply in tandem with the mortality episode of the late 1990s and early 2000s, as has been reported for Arizona populations of *G. morafkai* (Chapter 5).

As elsewhere in *G. morafkai* populations (Chapters 2, 4, and 5), the mortality episode and large apparent reduction in abundance that we observed occurred in tandem with drought and high temperature. Although the general warming trend in our study region closely mirrors that in Arizona, details of the drought period during which we worked are slightly different from the Arizona drought, which reached

or approached a record-setting nadir in 2002 throughout most or all of the state's desert and semi-desert lowlands (the desert lowlands of northwestern Sonora show a precipitation pattern similar to that of Arizona; Fig. 3.4). A summary of mortality episodes in *G. morafkai* in Arizona (Chapter 5) revealed just one incident clearly associated with the 1995-1998 drought period; however, the available climate data indicate that drought timing and severity, as well as high temperatures, near our study areas were more severe in the late 1990s than in 2002. We believe the observed mortality episode in 2001-2002 was ultimately related to drought and rising temperatures.

Proximate causes of the mortality we documented are not known. As Reyes Osorio and Bury (1982) noted, there is no livestock grazing on Tiburon, yielding what they interpreted as optimal conditions for tortoises. Although livestock grazing occurs on the coastal mainland, we observed high mortality in both settings. Although drought conditions existed in the 1970s, they were not severe, as was also the case from the late 1990s to at least 2002; however, mean annual temperatures were lower by about 1.6C and annual mean daily high temperatures averaged were lower by about 3°C (Fig. 3.3). Thus, aridity during our study period was exacerbated by elevated temperature, so ecological drought was likely more severe. If there were direct effects of temperature (overheating or thermal restriction of hours of activity [Sinervo et al. 2010]) on tortoises, rising temperatures may have been a contributing factor in the mortality episode.

Another proximate cause for the die-off may be disease. Although not commonly seen in desert tortoises in Sonoran Desert (Dickenson et al. 2001, 2002, 2005; Jones 2008; Berry et al. 2014, *in press*), we observed clinical signs of upper respiratory tract disease at one of our study plots, though we did not attempt to identify a pathogenic cause. Elevated disease frequency or severity have not been identified in association with other mortality episodes and declines in *G. morafkai*, and it is possible that symptoms we observed were ultimately related to physiological stress related to climatic conditions (Peterson 1994, 1996a&b). Other unknown causes for this catastrophic die-off may be yet to be discovered.

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Chapter 4 **Post-Drought Population Resurvey of Desert Tortoises (*Gopherus morafkai*) in Southwestern Arizona**

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ABSTRACT

We used repeat-transect and a repeat-plot search in 1995-6 and 2005-6 to measure response of *Gopherus morafkai* abundance over a 10-year period including drought-of-record at Organ Pipe Cactus National Monument in southern Arizona. Rising temperatures since the 1960s reached a high point during our study period. Large mortality episodes and major abundance reductions were recorded at four other *G. morafkai* census sites in Arizona and Sonora during 1999-2003. Further, the transitional environment at OPCNM, where there is a steep gradient from relatively mesic to highly arid desertscrub, may be expected to increase the likelihood of detectable drought effects on biota. Thus, based on a hypothesis that desert tortoise population declines are caused by drought (low rainfall and high temperatures) we predicted that a marked decline in observed abundance would have occurred during the duration of this study. We used a GIS project to translate GPS-based, hand-drawn transects from 1995 into repeat-transect tracks followed using hand-held GPS units in 2005. We also repeated the first pass in 1996 from a multi-pass 1-km² plot census to a matched pass in 2006. We compared data, controlling for distance and search effort over time, for live tortoises, carcasses (as a percentage of live + dead totals), and tortoise sign. In 2005-6 we were able to closely match 1995-6 effort in time, distance, location, and habitat. We found 21 live tortoises in 1995-6 (0.136/km) in and 18 tortoises (0.107/km) in 2005, a 21% decrease that was non-significant; total sign encounter rate decreased by only 8%, also non-significantly between survey decades (0.446/km in 1995-6 and 0.409 in 2005-6); and more carcasses were found in 1995-6 (n = 8) than in 2005-6 (n = 4). However, in 1995-6, a significantly lower proportion of tortoises and sign were found on bajadas (compared to rock slopes) than in 2005-6, suggesting that a behavioral change toward greater use of moisture-holding soil burrows or otherwise superior bajada habitat may have occurred in response to increasing temperature and aridity. The fraction of carcasses in the 1995-6 sample (21%) was not significantly different from that in 2005-6 (13%), but both sample fractions were significantly lower than in a foregoing survey in 1988-90 (37%), which we interpret to represent an earlier episode of high mortality and population decline at OPCNM, synchronous with mass mortality episodes in three mountain ranges north of OPCNM on the same steep ecological gradient. Although this apparently extensive area of large scale mortality is cause for conservation concern, we speculate that following major drought-related population declines, *G. morafkai* populations may transition to lowered abundance and then be buffered to some extent against further effects of droughts, even relatively severe ones.

1.1 INTRODUCTION

1.1.1 Climate and Tortoise Ecology

Global warming is expected to continue through the 21st century (IPCC 2013), and, all-else equal, the already-warm American Southwest could suffer disproportionately. A growing consensus of climate models predicts an even more severe scenario – disproportionate warming in the region (Seeger et al. 2007; MacDonald 2010; Garfin et al. 2013) and, further, reduced precipitation, at least for winter-spring (Dominguez et al. 2010; Cayan et al. 2010; Seager and Vecchi 2010; Duffy et al. 2014; Swain and Hayhoe 2014), which many authors expect to produce a long-term drying trend in the Southwest through the century (Seager et al. 2007; Overpeck and Udall 2010; Seager et al. 2013). Recent findings suggest that extremes, notably drought duration and severity, are projected to increase with climate warming (Ault et al. 2012, 2013; Dai 2013) although this is still debated (Trenbeth et al. 2014). Ecosystems will be disrupted by such change (Breshears et al. 2005; McAuliffe and Hamerlynck 2010; Munson et al. 2012), and the pace of change is likely to exceed the ability of impacted species to adapt or disperse across fragmented landscapes in response (Sinervo et al. 2010). This will be especially problematic for species with low motility and long generation times such as turtles. It may prove impossible to preserve species by simply setting aside existing habitat in preserves. Absent new initiatives to freeze the current trajectory for increasing anthropogenic contribution to climate change, novel, large-scale, active conservation measures will be required to preserve biodiversity. Such measures will put premiums on causal understanding and monitoring to support ecological management.

The catastrophic decline of the desert tortoise in the Mojave Desert over the past three decades (likely exceeding 90% decline in abundance over wide areas; Berry 1984a, 2003; Berry and Burge 1984; Berry and Nicholson 1984a; Bury and Corn 1995; Tracy et al 2004; USFWS 2011) has led to the listing of the “Mojave tortoise” (now recognized as a full species, Agassiz’s Desert Tortoise, *Gopherus agassizii*; Murphy et al. 2011) as a threatened species (USFWS 2011a). Well-supported putative causes of major tortoise declines in Mojave Desert include: (1) elimination of recruitment via predation by human-subsidized raven populations on small juvenile tortoises (Boarman 2002; Kristan and Boarman 2003); (2) massive predation by coyotes, likely also human-subsidized, on adult tortoises during drought-related predator-prey cycle events (Berry et al. 2002, 2006; Esque et al. 2010); (3) mass mortality of adult tortoises infected by disease (Jacobson et al. 1991, 1995; Berry 1997; Homer et al. 1998); and (4) highway mortality (Boarman and Sazaki 2006). Many other plausible causes of decline have been identified (Boarman 2002; Tracy et al. 2004; USFWS 2011), including poor nutritional status due to livestock grazing, but have not been rigorously connected to population declines. These declines in the past three decades have occurred during a period of increasing heat (Seager et al. 2007; Hereford et al. 2006) and often during drought that might be an ultimate driver of population collapses (Peterson 1994, 1996a&b; Henan 1997; Henan et al. 1998; Longshore et al. 2003, Karl 2004). Elucidation of ultimate causes of many catastrophic declines, or of successful recovery programs, remains elusive (USFWS 2011a).

Desert tortoise populations in the Sonoran Desert (Morafka’s Desert Tortoise, *G. morafkai*) have also declined in recent decades (USFWS 2010), but causation remains largely unknown. While disease, primarily associated with *Mycoplasma* bacteria has been implicated in declines in Mojave Desert, no

comparable disease problems or die-offs are reported for Sonoran Desert (Dickenson et al 2002, 2005; Jones 2008; Jones et al. 2005). Burgeoning urban sprawl and buffel grass invasion with intensified fire regime (Esque et al. 2002, 2003) and stress to tortoise homeostasis (Gray 2012) may locally threaten tortoise populations in the Sonoran Desert, but cannot explain most or many of the major observed declines. Populations appeared or were reported as mostly stable as recently as 1999 (Averill-Murray et al. 2002; Boarman and Kristan 2008; USFWS 2010), although Zylstra et al. (2012) demonstrated that proximity to incorporated human communities was associated with lowered tortoise survivorship.

By 2002 it had become clear that additional population reductions had occurred on some of the 17 long-term study plots in Arizona (Boarman and Kristan 2008; USFWS 2010; see Chapter 5). We have further evidence of catastrophic mortality events associated with droughts: Maricopa Mountains (Wirt and Holm 1997a), Sand Tank Mountains (Wirt and Holm 1997b), and Saucedo Mountains (Dames and Moore, Inc. 1994) during late 1980s to ca. 1990; Ironwood Forest National Monument (R. Repp, in Rosen 2003) in 1996; locally in Tohono O'odham Nation (Rosen and Holm, unpublished) ca. 2000-2001; and at and near Tiburon Island in Sonora (M. Vaughn, unpublished) in 1998-2002; summarized in Chapter 5. Many of these declines occurred in relatively arid habitat, including that associated with the transition between the arid Lower Colorado River Valley (LCV) and the less arid, thornscrub-like Arizona Upland (AZUP) phytogeographic provinces (Brown 1982) of the Sonoran Desert. The timing of all these major mortality events corresponds to drought conditions during the past three decades, which occurred in the early and late 1980s, mid-late 1990s, and early 2000s (Figs. 4.1 and 4.2). Further, tortoises are less abundant and widespread in the LCV than AZUP (Averill-Murray et al. 2002; Van Devender 2002; Boarman and Kristan 2008), suggesting that spreading aridity and increasing temperatures may combine (Weiss et al. 2012) to threaten the tortoise in the Sonoran Desert.

Zylstra et al. (2012) further demonstrated that dry conditions were associated with reduced survivorship on 17 long-term study plots in Arizona, and that this effect was strongest for populations in low-elevation, more arid places. We can therefore hypothesize that intensifying drought, alone or, notably, exacerbated by rising temperatures (Breshears et al. 2005), will result in continued or elevated tortoise mortality. On the Maricopa Mountains study plot, tortoise population collapse in the late 1980s occurred as rising temperatures approached a late-20th century maximum, contributing to severe drought as indexed by the Palmer Drought Severity Index (PDSI); however, a substantial proportion of the observed tortoise remains appeared to represent deaths preceding the late 1980s drought (Wirt 1988, 1995; Wirt and Holm 1997a). Subsequent data indicate that further die-offs and decline have not occurred there (Averill-Murray et al. 2002; Boarman and Kristan 2008; see Chapter 5). Although it has been suggested (Averill-Murray et al. 2002; C. Schwalbe, pers. comm.) that the Maricopa collapse may have been associated with extreme, highly localized rainfall failure, the event was apparently more widespread, including both the Sand Tank and Saucedo Mountains (Wirt and Holm 1994 (in Geo-Marine 1994), 1997b; Dames and Moore 1994).

The pattern and dynamics of tortoise population reductions in Sonoran Desert have not been systematically discussed since Wirt (1995) and Wirt and Holm (1997a&b), although Zylstra et al. (2012) provide critical clues. Whether the most important declines are usually or always catastrophic, and whether recurrent drought conditions result in continuing reductions are unknown.

We identified circumstances at Organ Pipe Cactus National Monument (OPCNM) that might allow us to examine some of these climatic impacts on the desert tortoise in the Sonoran Desert. OPCNM lies astride a transition between LCV and the AZUP provinces (Brown 1982), where mortality-associated population reductions may be expected as a result of the variation in rainfall. Annual rainfall in much of the LCV is 25-213 mm whereas it is typically 250-305 mm in the AZUP. Across southern Arizona, rainfall drops from 317 mm at Tucson to 82 mm at Yuma (0.682 mm/km), whereas the drop over 25 km across OPCNM is about 264 mm to 192 mm (about 2.937 mm/km) or ≥ 4 times steeper (data from NOAA and OPCNM), as noted by Comrie and Broyles 2002). These patterns primarily reflect the elevational gradient at OPCNM, as well as storm tracks (Sellers and Hill 1974; Sellers et al. 1985), and, on a broader scale, approximate the climatic transition from the tropical monsoon to desert precipitation regimes (Comrie and Glen 1998). Baseline (mid-valley) elevations remain relatively unchanged from Tucson west across the Tohono O'odham Nation, and drop gradually from west of the Quitobaquito Hills at OPCNM and adjoining Agua Dulce Mountains to Yuma near the Colorado River, whereas they drop rapidly across

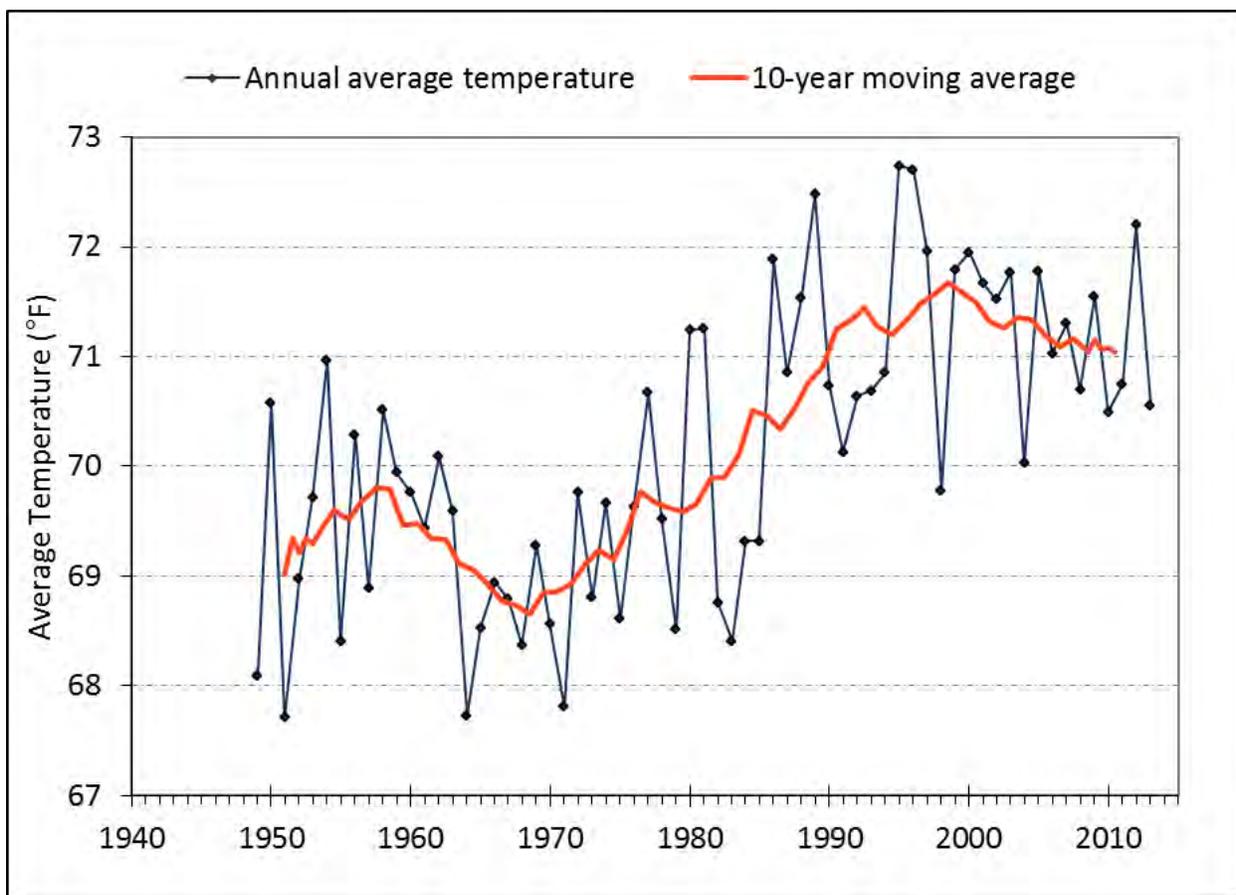


Figure 4.1. Long-term temperature trend measured at headquarters, in the central-eastern portion of Organ Pipe Cactus National Monument, Arizona, 1949-2013. The general trend closely monitors that for the American Southwest.

We hypothesize that drought and high temperatures are primary drivers of tortoise abundance and, notably, of population reductions in the Sonoran Desert region. If this is correct, rising temperatures (Fig. 4.1) and the 2001-2002 record-severity drought at OPCNM (Fig. 4.2) might have

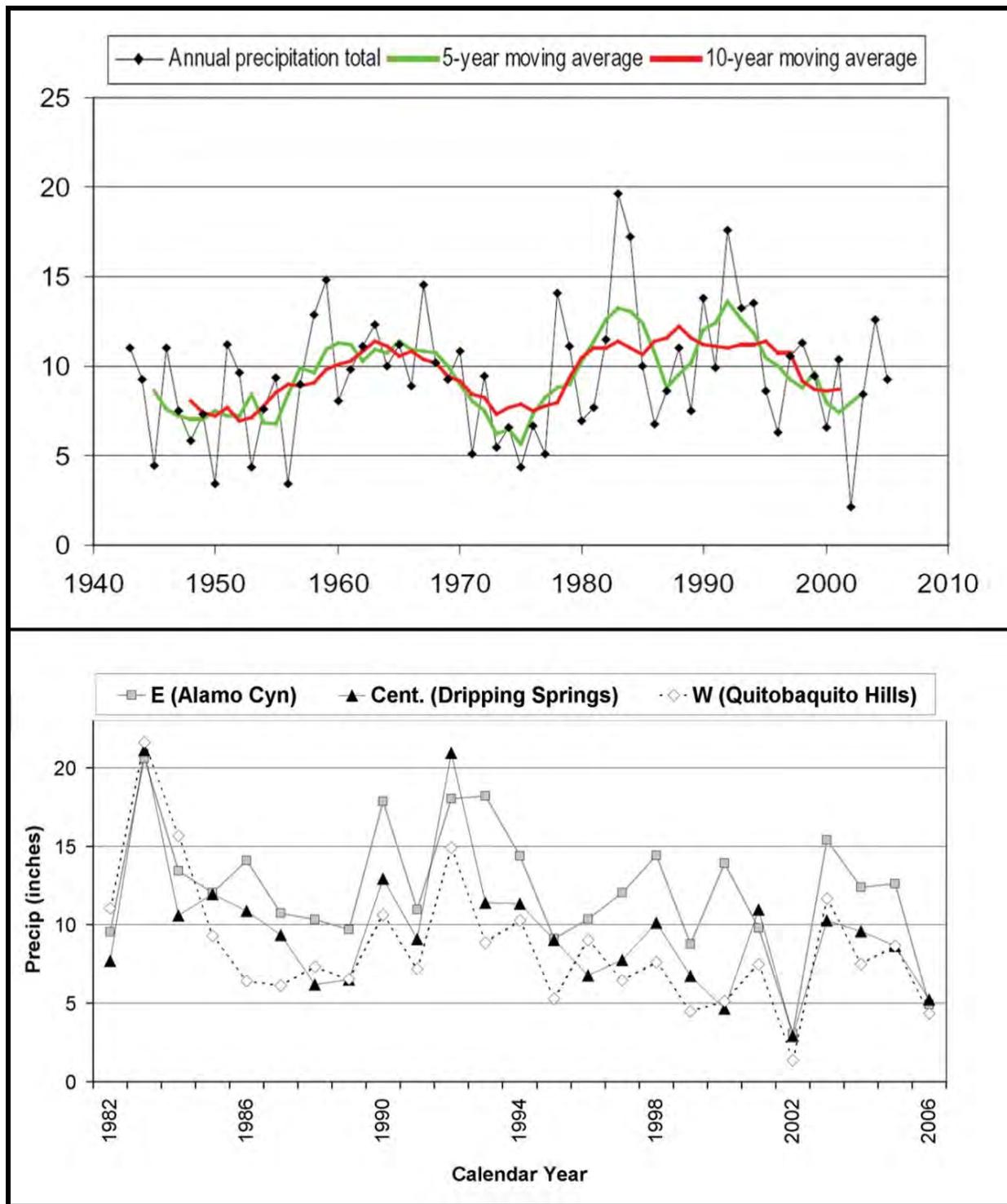


Figure 4.2. Precipitation trends and patterns at Organ Pipe Cactus National Monument, Arizona, based on rain gauge readings at headquarters (top) and three other stations representing the transition across the monument (bottom). For all but one site among 21 monitored, 2002 was the driest year on record at OPCNM.

had profound demographic impacts on tortoise populations there. In this paper, however, we show that tortoise populations at OPCNM did not collapse, and did not decline steeply, if at all, during this severe

drought, although they may have responded by an ecological or behavioral shift. Further, we present evidence that the tortoise population at OPCNM experienced one or more previous mortality events. The pattern of decline at OPCNM, like that in the Maricopa Mountains, may reflect a state transition from higher abundances found in the AZUP core of tortoise habitat in the Sonoran Desert of Arizona (see Averill-Murray et al. 2002; and Chapter 5) to lower abundance more characteristic of the LCV margin.

4.2 METHODS

4.2.1 Monitoring Approaches

A variety of monitoring methods have been applied in conservation biology of the desert tortoise: both 1-mi² and 1-km² survey plots (Averill-Murray 2000); distance sampling with radiotelemetry (Averill-Murray and Averill-Murray 2005), occupancy (presence-absence) modeling (Zylstra 2009; Zylstra and Steidl 2008, 2009; Zylstra et al. 2010); and sign transects (USFWS 2011). Each of these methods has drawbacks. The plot method is time and labor intensive and precludes broad landscape coverage. Distance sampling and occupancy modeling are also time and labor intensive; they deliver good abundance information but, like sign transects yield limited demographic information. As a result of arguments over these various methods, agreement about desert tortoise declines – even widespread, catastrophic declines – has been inordinately elusive, for both Mojave Desert (Bury and Corn 1995; USFWS 2011a) and Sonoran Desert (Boarman and Kristan 2008; USFWS 2010 and therein) tortoise populations. While statistically satisfying, and promising (Zylstra 2009; Zylstra and Steidl 2008, 2009; Zylstra et al. 2010), the methodological upheaval has unfocused what now appear to be widespread, steep declines in both deserts.

A primary limiting factor in desert tortoise monitoring, which we encountered, is a survey time and funding constraint on sample size, especially for live animals. In this paper, we report results from relatively simple, repeatable methods to maximize both sample size, especially of live tortoises, and depth of historical interpretation that cannot be obtained with newer, better methods and cannot be used to interpret the first 2-3 decades of intensive observation during which major declines have already occurred, as described above (see Introduction). Three 1-km² plots were established at OPCNM in 1996-7, and a transect baseline dataset on tortoises at OPCNM using experienced-observer, optimal-search methods (i.e., high-grading) was established during 1988-1995. In this report, we present a 10-year profile of repeat-transect results from formalized optimal-search transect methods established in 1995 and redone in 2005 and a standardized 1-km² plot search in 1996 and 2006, as well as longer-term observations on tortoise mortality. Each approach is described in detail below.

4.2.2 Data Collected

For each transect or plot search, we recorded date, time, location, observer(s), macrohabitat (rock slope, bajada; xeroriparian bajada thornscrub, upland [non-xeroriparian] bajada desertscrub); time, temperature, and weather conditions; and dominant plant species. All surveys were conducted during August to early October, and individual areas were surveyed at seasonal points (± 2 wk). Based on our experience, all four years had adequate summer rainfall (Fig. 4.2) to support normal tortoise activity at the time the work was performed. For each tortoise observation we recorded burrow type, dimensions,

and orientation; time, temperature, and weather conditions; and tortoise size, sex, age class (juvenile, immature, adult), shelter site, and behavior.

We recorded each instance of tortoise “sign” found during transect and plot work as a GPS waypoint. Sign included (in addition to live tortoise) characteristic plant-filled tortoise scat (or scat groupings, counted as one “modified sign”), and active or recently used tortoise burrows with characteristic digging and dirt-mounding and contouring, including at potential rock shelter sites. Carcasses (typically shell remains) of dead tortoises (see below) were not counted as sign. We scored observations of scat sign as present ($n=1$ modified sign) or absent at a local (< 5 m radius) site. Burrows occupied by a live tortoise were noted, but only scored separately as sign if unoccupied and considered “active” based on presence of scat, tortoise tracks, or apparent tortoise digging.

We also analyzed additional data on live tortoises and remains found on repeat-transects and plots, plus totals from three additional data sources: a 1988-1990 monument-wide tortoise survey at OPCNM, transects and plot searches carried out in 1995-1997 and not repeated in 2005, and highway transects established and carried out in 2005 reported elsewhere (Rosen and Holm, *manuscript*).

4.2.3 Optimal-Search Transects

The 1995 baseline monitoring surveys for this study comprised 50 backcountry transects representing a full range of likely and possible (unlikely) habitat for the desert tortoise. Each transect was carried out by one or more experienced field observers specializing in desert tortoise monitoring and research. At the conclusion of each 1995 transect, waypoints collected in the field were plotted, and each transect was hand-mapped onto USGS 15-minute topographic maps.

In 2005, a group of similarly experienced field biologists repeated 25 of the original 50 1995 transects (Fig. 4.3). The 25 selected transects were in occupied habitat, as determined by the 1995 survey, excluding middle and lower bajada environments that were included *pro forma* in 1995 and confirmed as non-habitat. We further eliminated some transects considered unsafe due to international smuggling activity. Tracks from the topographic maps were digitized using ArcGIS™, loaded into GPS units, and followed by fieldworkers in 2005. To replicate the 1995 effort, fieldworkers were instructed to follow the tracks but deviate up to 75 m to investigate apparently suitable microhabitat features (Fig. 4.3) that 1995 workers would most likely have investigated, to account for the imprecision of the 1995 mapping and to conform to the optimal search method used in 1995. Within these constraints, we searched for tortoises (by looking in burrows as well as finding surface-active tortoise), shell remains, and scat sign left by tortoises, again as was done in 1995 monitoring protocol.

Safety concerns prompted us to work in pairs most of the time during 2005. We used two protocols when working in pairs in 2005. In most cases, the pair worked in opposite directions in the transect loop, and upon meeting hiked out without collecting additional data. In three cases safety concerns dictated that two surveyors remain within earshot; in these cases, they worked the same transect but remained separated by approximately 50-100 m, and each person’s work was considered a separate repetition of the transect.

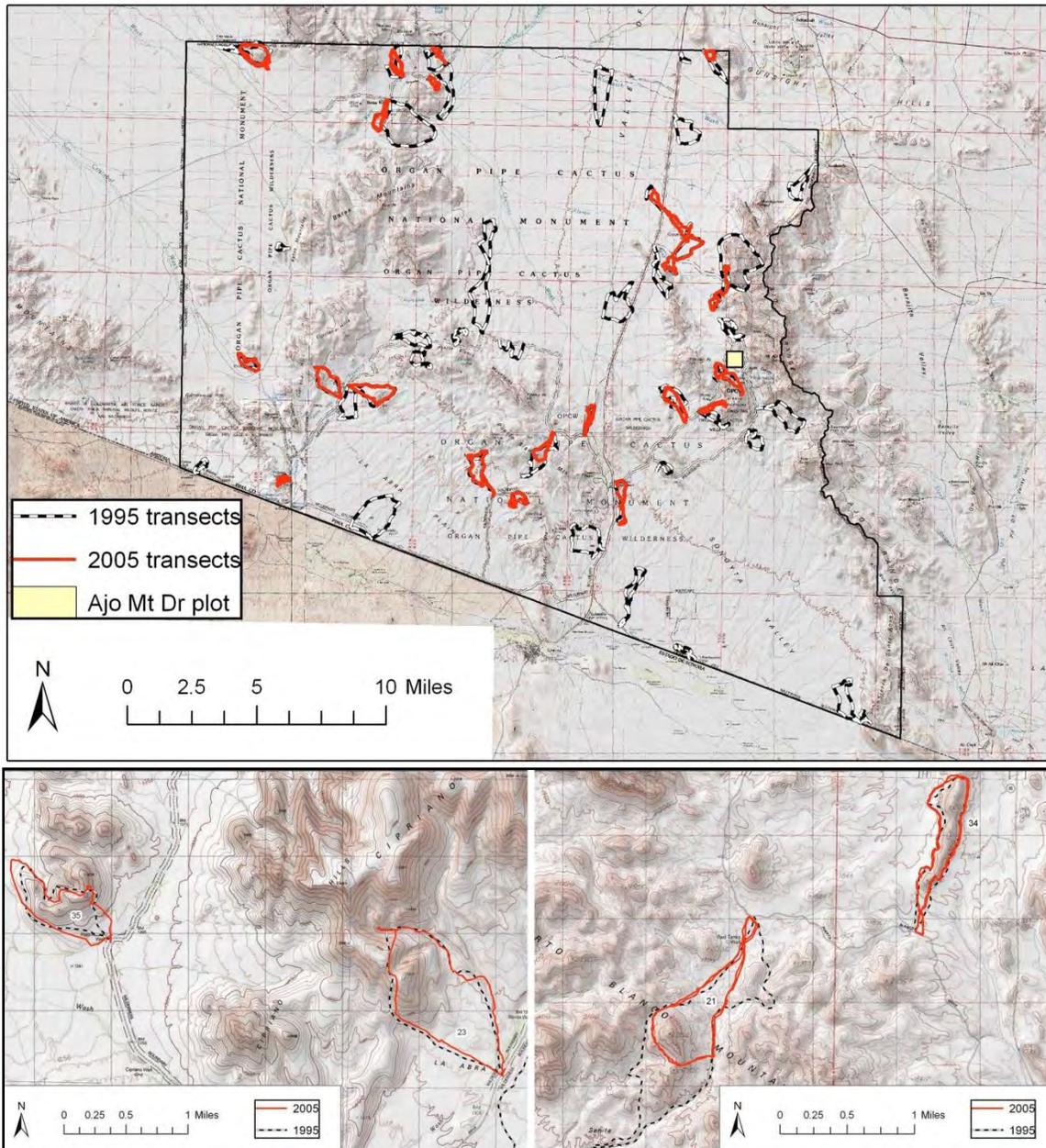


Figure 4.3. Desert tortoise repeat transects (2005) overlain on original transects (1995) at Organ Pipe Cactus National Monument, Arizona. A 1-km² survey plot monitored in 1996 and 2006 is also shown, as a yellow square (above). Closer views of four of the transects (below).

Based on a pre-existing GIS model of tortoise habitat type and quality at OPCNM (OPCNM, unpublished), we used ArcGIS layers to classify transect environments as unoccupied (higher mountain slopes, sandy middle to lower bajadas, and flats) or occupied (lower rock slopes, upper-middle bajada xeroriparian arroyo margins, upper to middle bajada upland). We post-processed all 25 tracks in ArcGIS for both 1995 and 2005 datasets. Macrohabitat categories were assigned in ArcGIS as follows.

The distinction between rock slope and bajada environments was based on an overlay of slope, geology, and soil raster layers. Slope (S1) was assigned a value of 0 for slopes of 0-10 degrees and a value of 1 for

slopes of 11 or more degrees. Geology (S2) was assigned value of 0 for surficial deposits and a value of 1 for rocks. Soil (S3) was assigned a value of 0 for all non-rockland and a value of 1 for rockland. Each cell was classified as rock slope for sum (S2+S3) of 2 or 3 and classified as bajada for a sum of 0 or 1. Bajada cells were classified as bajada xeroriparian if they fell within the 20 meter buffer of washes and arroyos in the hydrology layer. Otherwise, bajada cells were classified as upland bajada. Although upper-middle bajada upland (non-xeroriparian Sonoran desertscrub) habitat is little used, its close proximity to heavily used xeroriparian habitat required that we include it. Our ArcGIS analysis estimated that 79.7% of bajada encounter records originated in xeroriparian habitat, whereas habitat records in the annotated field datasheet used in 2005 showed that all records on bajadas proper (see Discussion section) were from or closely adjacent to xeroriparian environments. We report encounter rates for all bajada habitat, but in our summary ANOVA we reduced macrohabitat categories to two (rock slopes and bajada) to eliminate small sample size effects in the bajada upland (non-xeroriparian) category.

We categorized transects within OPCNM as eastern (n = 12 transects) and western (n = 13 transects; Appendix A), and identified nine clusters of transects within local geographic areas within OPCNM with generally similar characteristics of precipitation, geology, and vegetation (Appendix A).

4.2.4 Plot Re-survey

We selected one of the three 1-km² survey plots from 1996 for re-survey in 2006. This plot, in the western base of the Ajo Mountains range in eastern OPCNM, was thoroughly searched five times in 1996, but only once in 2006, so we compared the 2006 result only to the first 1996 plot search. In both years, the pass over the plot consisted of a systematic search within 9 subplots comprising the 1-km² plot. As with the transects, plot surveys in 1996 and 2006 were conducted by experienced tortoise field biologists, with data collection and scoring as described above except that scat and burrows were not recorded.

4.2.5 Mortality Observations

We recorded each instance in which a tortoise remain was found during 1995-1997 and 2005-2006 as a GPS waypoint. The 1997 records were the completion of census plots started in 1996, and were not part of the comparison encounter rates between decades, as only the first pass (1996) was compared to the single 2006 pass. For data from 1988-1990, tortoise observations were recorded with verbal localities only. Localities for these records were placed with sufficient detail to identify general location within OPCNM (eastern, central, or western areas, as defined for this paper, and named rocky slope features on 7.5-minute USGS quadrangle maps).

In 1995, some field workers searched for remains of dead tortoises by raking through packrat middens, which we did not do in other surveys. These instances were carefully noted in the data and were excluded from data and analyses presented herein. We also considered the possibility that identification of tortoise burrows/shelters in rock slope settings, where natural rather than excavated features are often used by tortoises, presented possible inconsistencies, and therefore performed analyses with and without these shelters. Results were unaffected by this possible bias, and all the shelter data were therefore included in the presentation here.

Analysis. Statistical analysis was performed using SAS JMP. We first performed univariate and graphical analyses to examine effects and normality in Microsoft Excel or JMP. Chi-square (Yates corrected) testing of 1995 versus 2005 was performed on all data combined, adjusting for slight differences in total length of transect performed in the two years. For some analyses, we grouped the transects into 9 clusters corresponding to major geologic and geographic features of OPCNM (Appendix I). The resultant data were examined graphically for deviations from normality, and a full-model analysis of variance was then used to summarize the findings.

4.3 RESULTS

4.3.1 Survey Methods

Field personnel were able to retrace most of the selected 1995 routes in 2005 (Fig. 4.3). With the exception of the three transects that were run by two surveyors in tandem (totaling 12.6 survey km), the total survey length differed by only 1.5% between the years. The distribution of effort by macrohabitat did not differ significantly between years, and was closely similar (Table 4.1).

Table 4.1. Linear distance of desert tortoise survey transects worked in both 1995 and 2005 at Organ Pipe Cactus National Monument, Arizona. The transects were run once each in 1995; 3 of the 25 transects were run twice in 2005.

Habitat Category	1995		2005	
	Transect Distance (km)	% of Effort	Transect Distance (km)	% of Effort
Rock Slope	34.5	22%	37.6	22%
Bajada Xeroriparian	32.3	21%	34.1	20%
Bajada Upland	87.9	57%	96.9	58%
Bajada (Overall)	120.2	78%	131.0	78%
Total	154.7		168.6	

4.3.2 Total Observation Rate in 1995 and 2005

In 2005, we found 18 live tortoises in 168.6 km (0.107 tortoises/transect-km) in 2005, which is 79% of the encounter rate in 1995 (21 live tortoises on 154.7 km; 0.136 tortoises/transect-km; Table 4.2) but not significantly different ($\chi^2 = 0.59$, $df = 1$, $p > 0.4$). Combining these results with those from the 1-km² plot (Table 4.3), 25 live tortoises were found in 2005 compared to 32 in 1995, also not a statistically significant difference ($\chi^2 = 1.36$, $df = 1$, $p > 0.2$). There was no difference in total sign between the 1995 and 2005 (Table 4.2).

Although we found 2 tortoise carcasses during 2005 while performing similar transects for a highway-effect study, we found none in 2005 re-survey of the 1995 transects, where 6 remains were found in 1995; combining these data with the 1-km² plot data gives 4 carcasses in the 2005 survey and 10 in 1995 (Table 4.4; $\chi^2 = 1.33$, $df = 1$, $p > 0.2$).

Table 4.2. Results for 25 repeated desert tortoise survey transects in Organ Pipe Cactus National Monument, Arizona.

Survey Year	Transect Km	Tortoise Sign			Total Sign	Shell Remains
		Live Tortoises	Scat	Burrows		
<u>1995</u>						
Rock Slope	34.5	8	14	12	34	2
Bajada	120.2	13	6	16	35	4
1995 Total	154.7	21	20	28	69	6
<u>2005</u>						
Rock Slope	37.6	4	7	9	20	0
Bajada	131.0	14	16	19	49	0
2005 Total	168.6	18	23	28	69	0

Table 4.3. Results of single survey passes on a standardized 1 km² desert tortoise study plot in rock slope habitat repeated after a 10-year interval at Organ Pipe Cactus National Monument, Arizona.

Observation Type	Year	
	1996	2006
Live tortoises	11	7
Shell remains	2	4
Total	13	11

4.3.3 Macrohabitat and Geographic Comparison of 1995 and 2005

Live tortoise encounter rates on transects were higher on rock slopes than bajadas in 1995 (0.232/km vs. 0.108/km) but not in 2005 (0.106/km vs. 0.107/km). For all sign (including live tortoises), encounter rates were higher on rock slopes than bajadas in both sampling years (1995: 0.986/km vs. 0.291/km; 2005: 0.532/km vs. 0.374/km). However, considering only the xeroriparian component of bajada habitat, total sign encounter rates were similar for the two macrohabitats in 1995 (0.986/km vs. 0.864/km) but lower for rock slopes than bajada xeroriparian in 2005 (0.532/km vs. 1.145/km).

Whereas approximately equal numbers of total sign observations were recorded in rock slope and bajada macrohabitat during 1995 transect work, in 2005, bajada environments yielded twice as many records as rock slope environments (Table 4.2 and Fig. 4.5). The macrohabitat difference between 1995 and 2005 was not statistically significant for live tortoises alone ($X^2 = 1.81$, $df = 1$, $p \approx 0.15$), but was significant for all tortoise sign ($X^2 = 5.91$, $df = 1$, $p < 0.02$).

We observed tortoises and sign at higher rates in the less arid eastern part of OPCNM than in the more arid western area (Table 4.4), as was reported by Wirt et al. (1999) for the 1995-6 surveys and the earlier 1988-1990 survey. Analysis of variance revealed significant variation in tortoise sign encounter rates among the finer-scale geographic clusters of transects and between macrohabitat categories (Table 4.5). A significant interaction term for **Macrohabitat X Geographic Area** reflects the large bajada associated with the Ajo Mountain range compared to smaller, less extensive bajadas in the population clusters we defined for other parts of OPCNM. The **Macrohabitat** effect reflects differences detailed in the two preceding paragraphs. The only significant effect involving decade-of-survey was the **Decade X Macrohabitat** effect, reflecting the decadal shift in observed tortoise activity away from rock slopes and onto bajadas.

Table 4.4. Observations of desert tortoise sign and remains on 25 repeated transects and one standardized plot search at Organ Pipe Cactus National Monument, Arizona, 1995-6 and 2005-6.

YR	East-West sub-region	Live Tortoises	Scat Instances	Tortoise Burrows	Total Sign	Dead Tortoises	Total Transect Length
<u>Total Numbers Observed:</u>							
<u>Transects (n = 25):</u>							
1995	W	6	12	17	35	6	98
2005	W	7	14	15	36	0	105
1995	E	15	8	11	34	2	57
2005	E	11	9	13	33	0	64
<u>1-km² Plot:</u>							
1996	E	11	--	--	na	2	na
2006	E	7	--	--	na	4	na
1995-6	Total	32	20	28	69	10	155
2005-6	Total	25	23	28	69	4	169
<u>Transect Observation Rate (no. / 10-km):</u>							
1995	W	0.62	1.23	1.74	3.59	0.62	98
2005	W	0.67	1.34	1.43	3.44	0.00	105
1995	E	2.62	1.40	1.92	5.95	0.35	57
2005	E	1.72	1.41	2.04	5.17	0.00	64
1995 transects overall		2.07	1.29	1.81	5.17	0.65	155
2005 transects overall		1.48	1.36	1.66	4.51	0.24	169

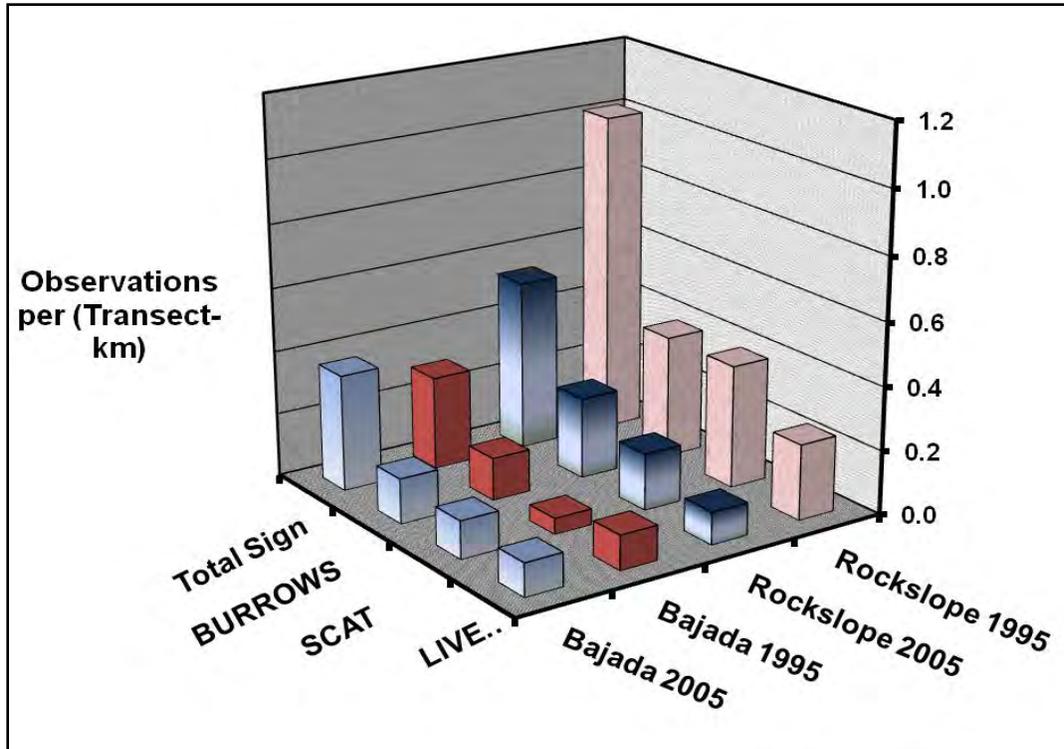


Figure 4.4. Monitoring results (observations / km) on 25 repeated transects at Organ Pipe Cactus National Monument, Arizona, according to macrohabitat.

Table 4.5. Analysis of variance of total desert tortoise transect observation rate (Σ [live tortoises + scat + burrows] / km) testing effects of decade (1995 vs. 2005), macrohabitat (rock slope, bajada), and eco-geographic cluster (see Appendix A). Significant effects are indicated by *.

ANOVA				
R ²	0.934		Root Mean Square Error	0.700
R ² Adjusted	0.712		Mean of Response	1.175
Observations	36			
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	27	55.6	2.058	4.2034
Error	8	3.9	0.489	<i>p</i> > F
C. Total	35	59.5		0.0201*
Source	DF	Sum of Squares	F Ratio	P > F
Decade	1	1.41	2.88	0.128
Macrohabitat	1	5.57	11.38	0.010*
Geographic Area	8	19.29	4.93	0.018*
Decade X Macrohabitat	1	2.64	5.38	0.049*
Decade X Geographic Area	8	4.94	1.26	0.375
Macrohabitat X Geographic Area	8	21.71	5.54	0.013*

4.3.4 Mortality Observations

Live and dead desert tortoise we observed at OPCNM during inventory and monitoring, 1988-2006 are shown in Table 4.6. Proportion of dead tortoises in 1995-1997 was significantly less than in 1988-1990 ($\chi^2 = 5.69$, $df = 1$, $p < 0.02$), and proportion dead in the 2005-2006 sample was significantly lower than in 1988-1990 ($\chi^2 = 7.17$, $df = 1$, $p < 0.01$) but not significantly lower than in 1995-1997 ($\chi^2 = 0.87$, $df = 1$, $p > 0.3$).

Table 4.6. Summary of all live and dead desert tortoises recorded during inventory and monitoring surveys at Organ Pipe Cactus National Monument, Arizona.

	1988-1990	1995-1997	2005-2006	Totals
Live	47	99	40	186
Dead	28	26	6	60
% Dead	37%	21%	13%	24%

4.4 DISCUSSION

4.4.1 Monitoring Approaches and Methods

We found 40 live tortoises in a region of moderate to low tortoise density (Wirt et al. 1999; Rosen and Lowe 1996; Lowe and Rosen 1992), in an extensive optimal-search survey that systematically covered eco-geographic variation across the study area. On a time (and cost) basis, our observation rate (0.12 tortoises/km, 0.16 tortoise/hr) was higher than that recorded using other methods at Tucson (e.g., 0.14 tortoise/person-hr; Zylstra et al. 2010) even though tortoise abundance at OPCNM (11-29 / km²) was about 2.2 – 2.7 times lower than near Tucson (Wirt et al. 1999; Averill-Murray et al. 2002; Averill-Murray and Averill-Murray 2005; Zylstra et al. 2010). The optimal-search (“high-grading”) approach was critical from the standpoint of sample size and cost limitations.

We achieved close matches between 1995 and 2005 transect surveys in distance and area covered and proportion of effort in major macrohabitat categories. Field personnel reported no major difficulty or delay associated with replicating past tracks, which we attribute to their extensive experience with both GPS equipment and tortoise field research. Freilich and LaRue (1998) suggested that observer experience may not be important for desert tortoise surveys, but Zylstra et al. (2010) found otherwise and we doubt that untrained observers could have carried out our protocol in a useful way.

We anticipate criticism that we cannot extend our inferences to the entire landscape of OPCNM because our transects were selected to be representative, rather than randomized. We counter this in four ways. First, had we randomly selected transect points and surveyed in rectilinear fashion, our encounter rates would have been greatly reduced. Second, we doubt there is a compelling reason to insist on precisely representing entire landscapes, given the massive effort and small benefit. In fact, intensive demographic, plot-based study of *G. morafkai* in Arizona, which was initiated in 1987, has essentially been discontinued since 2008 and resources shifted to highly labor-intensive presence-absence methods that lack historical depth and demographic relevance. Third, we assert that our knowledge of the

landscape and species' ecology cost-effectively represented the landscape by careful stratification. Lastly, given that desert tortoise ecologists in Sonoran Desert know already that much potential habitat is unsuitable for various reasons, we suggest that a stratified focus weighted toward habitat where the species is abundant is justified in the absence of clearly justified reasons to study poor habitat, one of which is discussed below.

Another potential criticism of our method is that tortoise activity might vary dramatically in response to environmental conditions, particularly precipitation. However, rainfall patterns and history during 1995-6 were similar to those in 2005-6. Summer precipitation is less variable than winter precipitation at OPCNM (variance for 1982-2013 was 50% higher for winter), and summer is usually a time of high and consistent (Averill-Murray et al. 2002) desert tortoise activity in Sonoran Desert. Although winter-spring precipitation does affect tortoise activity during and immediately following those seasons, tortoise activity in summer was not related to variation in summer precipitation (Averill-Murray and Klug 2000). We agree that more effort be placed on evaluating weather effects on tortoise detectability, although it is unlikely to have influenced our key findings in this case.

Our attempts to classify habitat *post facto* using GIS analysis resulted in fewer than half of bajada tortoise waypoints classified as within 20 m of a mapped wash in a 2006 hydrology layer at OPCNM. Using a georeferenced 2006 aerial image, or manually assigning points using ArcMap™ Bing™ imagery, 77% and 79%, respectively, were assigned to the xeroriparian bajada category. This suggests that post-processing of habitat association using existing GIS layers may be misleading in some cases, whereas precise results required more laborious use of aerial imagery.

Observations classified by post-processing as bajada upland were at or near the base of rock slopes, suggesting a distance buffer might be needed to distinguish rock-associated tortoises near slopes from tortoises utilizing burrows or foraging on upland interfluvies on upper-middle bajadas. As a result of these problems, we collapsed all bajada observations into a single category for analysis, since the proportion of effort for upland versus xeroriparian bajada habitat was virtually identical among years of the study. GIS post-processing could be improved by (1) creating GIS layers that precisely reflect the area of xeroriparian environments rather than distance-buffered drainage line feature, and (2) buffering the resultant xeroriparian category using empirically determined distances. However, precise field recording of macrohabitat remains necessary.

4.4.2 Mortality and Abundance Trends for 1995-6 to 2005-6

Our standardized dataset had more tortoise carcasses 1995-6 ($n = 10$) than 2005-6 ($n = 4$), though not statistically so. Considering all inventory and monitoring we have done at OPCNM, the percentage of carcasses in all tortoise records (live plus dead) was higher in 1995-1997 (21%) than 2005-2006 (13%), though again not significantly different. Consistent with these findings, we found a non-significant decline in tortoise and sign observation rates from 1995-6 to 2005-6. The severe early 21st century drought at OPCNM, which reached maximal severity in 2001-2, did not produce major tortoise mortality or population decline as we had predicted.

The period 1977-1984 contained the wettest years on record at OPCNM (Fig. 4.2), with high winter and summer rainfall coming into synchrony during 1982-1983. This was followed by a 1987-1989 sequence

containing years of delayed-onset summer monsoonal rains (especially 1987) and the first seasonal drought during intensive Sonoran Desert tortoise research (winter 1988-89 – July 3, 1990) after years of adequate to above-average rain (Fig. 4.1; Rosen and Lowe 1996). The 1988-1990 drought involved above-average temperatures as well as poor rainfall; and tortoise die-offs in the Sand Tank, Saucedo, and Maricopa mountains regions to the north of OPCNM (Fig. 4.6) occurred then (Wirt 1995; Wirt and Holm 1997a). The 1990s saw five major El Niño-related spring blooms, four of which, along with two strong summer monsoons, were before or during 1995. However, regional temperatures that had been rising since the 1960s peaked in the latter part of the decade, remaining high during 1996-2006, when there were only three El Niño-related spring blooms and monsoonal rainfall was low and variable. This accounting of climate suggests why a tortoise die-off may have occurred during the late 1980s and why mortality may have declined thereafter in the early 1990s despite a 1996-7 drought that corresponded to record high mean annual temperatures (Fig. 4.1). From 1999-early 2003 the Sonoran Desert region experienced serious drought, with 4 seasons of near-normal rainfall and 5 below-average seasons, culminating in record low rainfall averaging only 50 cm across OPCNM in 2002.

Why, considering climate severity, was there no tortoise die-off or major population decline at OPCNM after the mid-1990s? We propose two potentially interconnected explanations. First, if the OPCNM tortoise population had already experienced a heat- and drought-related population reduction during the late 1980s, monument populations may have undergone a state-transition from a higher density, more characteristic of Arizona Upland habitat, to low density more usual in arid habitat characteristic of Lower Colorado River Valley habitat. Second, tortoises may display compensatory behavioral or other density-dependent responses following drought.

At OPCNM, both the 1995-7 and 2005-6 samples had significantly lower proportions of carcasses than the 1988-1990 survey period (37% dead), suggesting that a significant mortality event occurred earlier at OPCNM during the latter half of the widespread regional 1960s-1990s warming trend (Seager et al. 2007; MacDonald 2010; Woodhouse et al. 2010) and at OPCNM (Fig. 4.1). As in the Maricopa, Sand Tank, and Saucedo mountains, all near the LCRV-AZUP transition, the carcasses found during the late 1980s-early 1990s included intact shells indicating recent mortality during dry years, 1987-June 1990, and disarticulated and fragmentary remains from earlier mortality. Although the Maricopa Mountains population collapse has been described as unique or isolated, these data suggest that tortoise populations in the entire region, at least from near the international border at OPCNM, north through the Sand Tank and Saucedo Mountains to the Maricopa Mountains south of Phoenix, experienced large-scale die-offs and population reductions early in the drought sequence the region has experienced since tortoise population monitoring began in 1979-1980.

Data from OPCNM and the Maricopa Mountains demonstrate that moderate and extreme droughts subsequent to the late 1980s did not produce a continuation of large tortoise mortality events. At OPCNM and on other *G. morafkai* study areas that have been monitored during 1987-2008, through two or more major drought episodes, there is now evidence for major declines ($\geq 60\%$ decline) at 6 or more sites (approximately a third of the study sites; see Chapter 5). At none of these sites have major declines re-occurred. This may of course be by chance, since the randomized probability of two declines at a site would only be about 11%. However, four major declines moved populations from moderately

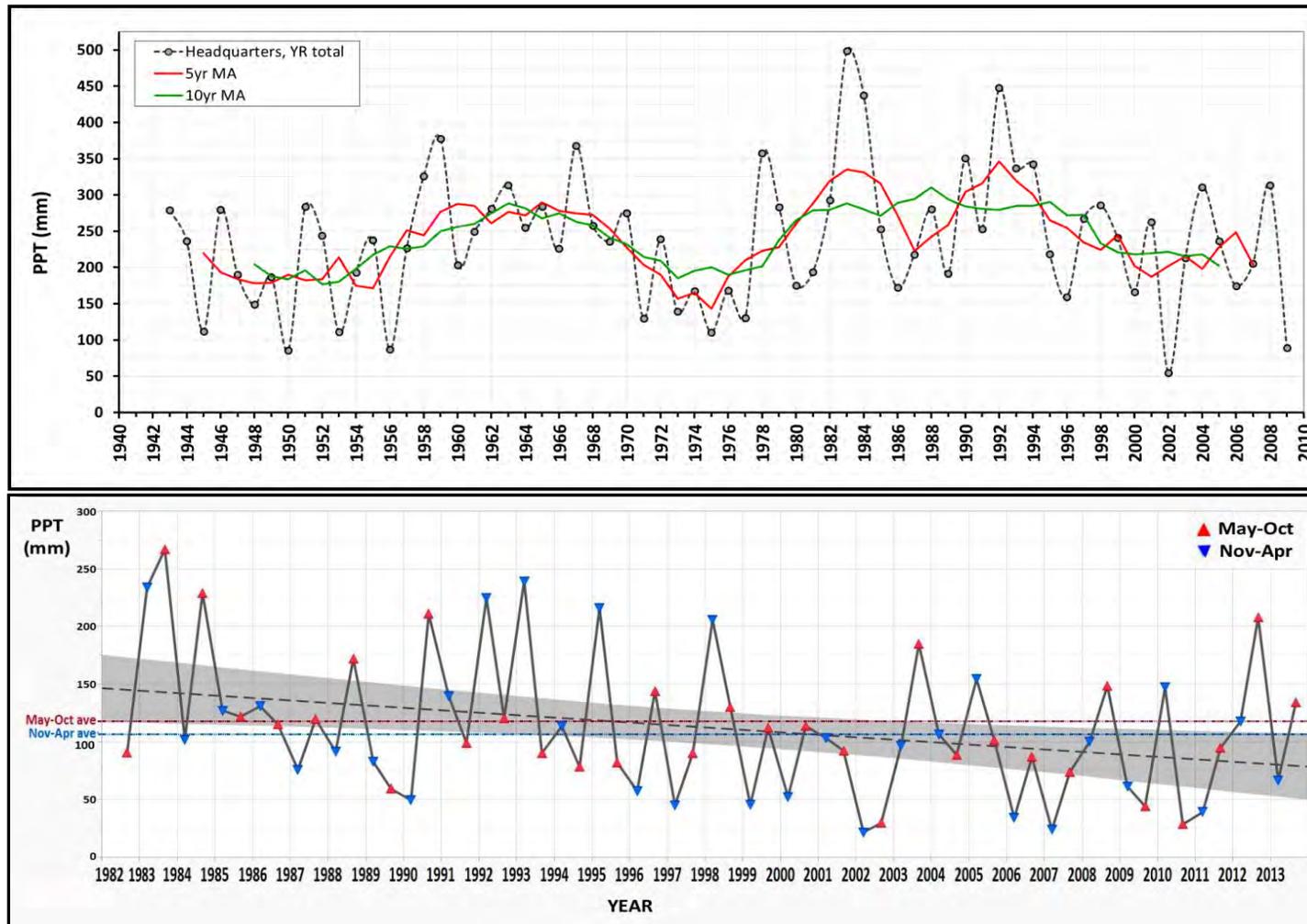


Figure 4.5. Seasonal precipitation history at Organ Pipe Cactus National Monument 1982-2013 from records for 19 sites throughout the monument. The seasons were defined to capture bi-seasonal (summer: July-September; winter-spring: November-March) rainy periods that produce fresh plant growth consumed by desert tortoises, although October rains may contribute to both seasons. Seasonal means depicted are for 1982-2013. Gray dashed line and light gray shading depict the trend, illustrated for this dataset, of decreasing rainfall during the period of intensive study of *Gopherus morafkai* in Arizona.

high or high abundance (estimates at \approx 46-150+ on mile square plots) to low abundance (estimates at \approx 10-45 adults and subadults, which is now characteristic of most sites in Arizona outside a geographic-ecological species core in the core of the Arizona Upland Sonoran Desert [Chapter 5]). For 13 censuses that have been reported after or during the 2005-7 drought, and abundance estimates declined for 4 of 9 populations that showed previous stability and only 1 of 4 populations that showed previous large declines. High densities currently remain in a geographic-ecological species core in the core of the Arizona Upland Sonoran Desert (Chapter 5). These results are consistent with a pattern of transition under a hot-arid climate period from high to low abundance followed by relative stability. Although this is not demonstrated conclusively, we speculate here that in the absence such a pattern the climate-related processes and declines we explore here and in Chapters 2,3 and 5 indicate a serious threat to the species and an extinction threat under at least some climate change scenarios. We suggest that populations at sites where there have been major, climate-related declines should *ceteris paribus* be more likely to suffer further declines, and thus we suggest that the transition pattern may be emerging, from high to low abundance with density dependence, in *G. morafkai* within good to moderately good habitat.

This ensemble of observations of abundance trends and mortality events at least weakly supports the hypothesis that effects of drought may be lasting, not only in reduced abundance, but also in resistance to further major decline. If not, the species appears to facing major threats.

Our data presented here suggest this for OPCNM, and may reflect a geographically widespread transition to low abundance in much of the range of *G. morafkai*.

4.4.3 Conservation Implications

Our discussion leads to a number of additional implications. First, the trend data for *G. morafkai* in high-quality habitat in the northern Sonoran Desert is clearly strongly negative (Chapter 5), but extinctions should be expected first in habitat of lower quality that has scarcely been studied. In the hot, extremely arid region of the lower Gila River Valley and Pinacate volcanic field, live desert tortoises are known from as few as three sites during the 21st century (Cristina Jones, Eugenio Larios, personal communications), one south of Wellton, Arizona, one each at Los Vidrios (Nuevos) and Sierra Suvuk, Sonora. However, carcasses and Wisconsin-age fossil desert tortoises are well known in lower Gila Valley (Van Devender 2002; McCord 2002), and spectacular but unstudied assemblages of fossil or subfossil tortoise remains are also in the area. Monitoring and – if live tortoises are found – demographic study should occur in this arid region to evaluate hypotheses that *G. morafkai* may be on a climate-driven extinction trajectory.

Second, if once a drought-related population crash has occurred, additional dramatic declines are thereby less likely, density-dependent population regulation may be occurring, as must be true, for any population not going extinct or to infinity, at some temporal scale. Yet density dependence has not been explored in tortoises. There are a number of plausible contributors to density dependence in Sonoran Desert tortoises. Variation in shelter quality and capacity, foraging habitat quality, and the spatial arrangement and proximity of these critical resources to each other and to water catchments for drinking seems a likely candidate mechanism for density dependence, but others can be postulated.

Third, the shift away from rock slope habitat to soil burrow use on adjoining bajadas indicated by our data suggests a behavioral hypothesis for post-decline stabilization of tortoise populations. In regions like OPCNM, where geomorphology is not ideal for the existing of high quality rock shelters for desert tortoises, humidity-buffering soil burrows (Bulova 2002) rather than the less buffered rock slope shelters may permit a behavioral shift that compensates for water stress associated with rising temperatures and drought. Recent reports demonstrate widespread use of bajadas (Riedle et al. 2008; Averill-Murray and Averill-Murray 2005) and in at least one case of valley floor soil burrows (Chapter 7), although it is not known whether tortoise habitat selection has changed over time. Data to test this should be available for at least 14 long-term monitoring plots for *G. morafkai* in Arizona (Chapter 5). Why such a change might occur after a major die-off or drought, rather than during it, is a logical question that points toward density dependence or other factors such as altered predation risk regimes as factors in habitat selection.

At present, little data exists that can be brought to bear on these issues, which are likely critical to understanding tortoise conservation biology and management. While recent reviews have correctly highlighted needs to understand early life ecology, survivorship, and recruitment in desert tortoises, our results and those from long-term and other study plots point toward a critical need to understand drivers of adult and subadult tortoise drought mortality and survival. Detailed habitat utilization studies coupled with demographics including survivorship and physiological ecology, including water and nutrient balance dynamics, are needed to evaluate the fate of and perhaps to save the desert tortoise in the Sonoran Desert.

4.5 MONITORING RECOMMENDATIONS

Several issues and hypotheses stemming from our work point toward additional study that may prove useful to conservation biology and management of the Sonoran Desert tortoise at OPCNM:

- Further investigate habitat use of bajadas and rock slopes:
 - Repeat transects in each habitat type, focusing on arroyos in bajada habitat.
 - Telemeter tortoises with access to both macrohabitats:
 - Measure burrow temperature, humidity, and utilization in both macrohabitats
 - Determine whether the extent to which individual tortoises use either or both rock slope and bajada habitats
 - Investigate aspect use on rock slopes under varying weather and climatic conditions (see Zylstra and Steidl 2008).
- Repeat transects and plots to estimate abundance on a 10-yr or shorter schedule.

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Appendix 1. Classification of transects into geographic clusters used in parametric analysis.

Cluster	Geographic Region	Transect Numbers	Geographic Area Description within OPCNM
1	W	25	Growler Mountains (NW corner)
2	W	30, 46, 49, 50	Bates Mountains- Growler Pass (NW section)
3	E	7	Gunsight Hills (NE corner)
4	E	2, 3, 4, 5, 39, 42	Alamo Canyon mouth and bajada (Ajo Mountains, NE section)
5	E	19, 33, 38, 40	Diablo Mountains (E-central section)
6	W	15, 21, 34, 43	Puerto Blanco Mountains (central mountain range)
7	E	14	Senita Basin (S-central basin)
8	W	23, 35, 48	Cipriano Hills (W-central range of low mountains)
9	W	11	Quitobaquito Hills (SW range of low mountains)

Chapter 5 **Observed Mortality Patterns and Population Declines in Desert Tortoises in the Sonoran Desert Region of Arizona and Sonora**

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Abstract

I evaluated the significance of published and new mortality evidence, in the form of carcasses of Sonoran desert tortoises (*Gopherus morafkai*), spanning nearly three decades of sampling through most of the species geographic distribution in Arizona, USA, and Sonora, Mexico. I extracted total capture counts, Lincoln-Peterson population estimates, carcass counts from reports from 17 repeat-census plots and several other single-census plots in Arizona. I also assembled other evidence of mortality episodes in the species obtained by us and others at other sites during fieldwork. I selected apparently valid estimates from the reports and analyzed these abundances by regression versus year, % of field samples found dead, and % of live samples that were juvenile (< 180 mm carapace length). Using estimates of time-since-death of carcasses in the reports, I constructed an aggregate profile over the 17 repeat-census plots of the total annual mortality represented by the carcasses. Regressions of abundance versus time show a highly significant aggregate decrease in abundance of approximately 50% in the repeat-census plots over 27 years, although methodological limitations make decline quantity uncertain. Using a regression of aggregate abundance versus year, I converted total annual mortality to an index of annual mortality rate over the plots in aggregate, and explored the correlation of mortality with climatic variables (annual precipitation, Palmer drought severity index [PDSI], and mean annual temperature). Episodes of mass mortality and large population reduction have been documented at 4 of the 17 repeat-census plots, and data suggest that lesser episodes of elevated mortality have affected several others. I report at least 6 additional instances where mortality episodes seem to have been accompanied by abundance declines. Abundance changes over time at the repeat-census plots, in aggregate and site-specifically, were strongly negatively correlated with percent of field samples found dead, but I did not find an effect of percent juveniles in the samples. In a sampling of this kind, the data suggest that field samples with $\geq 20\%$ dead animals indicate a high likelihood of accompanying decline in abundance. The top models relating changing abundance to climate were 2-year running mean and year-of-study annual precipitation, although 3-year running mean annual precipitation, year-of-study and 2-year running mean PDSI, and 2-year running mean annual temperature also showed significant linear regressions with abundance. Most episodes of unusually high mortality in *G. morafkai* have been co-temporal with drought. The species maintains (as of last records that range from 1997-2013 for various sites) relatively robust populations in a core region of Arizona Upland and Plains of Sonora Sonoran Desertscrub and has experienced either intense mortality or substantial population reduction, or both, in many regions peripheral to this core. Although no populations outside urbanized environments are known or thought

to have become extinct, little or no study has been conducted in the most climatically stressful part of the species distribution, where *G. morafkai* abundance is apparently lowest. The expression of anthropogenic global warming in the tortoise's range appears to be a credible threat.

5.1 Introduction

During an evaluation of status of *Gopherus morafkai* (Morafka's or Sonoran Desert tortoise) in northwestern Mexico, where it has been little studied, climate change stood out as a potential threat that would be ubiquitous, increasing, and serious (Chapter 1). Limited monitoring results for desert tortoises in Mexico required examination of results from throughout the species distribution to evaluate the significance of mortality observations of desert tortoises there. This evaluation is summarized here based on intensive monitoring at repeat-census study sites in Arizona and results reported from Mexico (Chapters 2 and 3) and elsewhere in Arizona (Chapter 4).

Recent reports show that other reptiles are vulnerable to anthropogenic global warming. Lizard activity and thence population viability are reduced by rising temperatures over large areas of Earth (Sinervo et al. 2010) and synchronous snake population declines of unknown etiology have recently been documented (Reading et al. 2010). Terrestrial turtles may be especially sensitive to warming effects on activity and warming-intensified drought because they are exposed to warming air and ground, and despite their surprising ability to cover ground steadily have limited ability to flee rapidly from heat. Similarly, despite their thermal mass inertia, terrestrial turtles have limited ability to thermoregulate by shuttling between sun and shade as lizards do. Finally, desert tortoises, and likely other terrestrial turtles in arid and semi-arid environments, are now well-known to be vulnerable to physiological stress during droughts, which are expected to become more frequent or severe in middle latitudes under anthropogenic global warming.

Large-scale and widespread declines of *Gopherus agassizii* (Agassiz's, or Mojave Desert tortoise) have multiple causes but are increasingly recognized to be drought-related (Berry et al. 2002; Field et al. 2007; Germano and Joyner 1989; Longshore et al. 2003; Lovich et al. 2014; Peterson 1994), although in some cases drought acts indirectly through elevated predation (Berry et al. 2002; Esque et al. 2010) or mortality sources are unclear (Germano and Joyner 1989). Recent climate-niche modeling (Barrows 2011) and long-term population study (Lovich et al. 2014) explicitly demonstrate a climate threat in *G. agassizii*. Other long-lived species with low mobility also show strong sensitivity to drought under the rising temperature climate regime in western North America (Breshears et al. 2005).

There remains less information on drivers of abundance in *G. morafkai*, which, unlike *G. agassizii*, is not federally listed and protected as a threatened species under the U.S. Endangered Species Act (ESA), although it is currently being evaluated for such protection (USFWS 2010). Previous reviews have suggested that *G. morafkai* is not experiencing major or widespread population decline (Averill-Murray et al. 2002; USFWS 2010) and a report to the contrary (Boarman and Kristan 2008) has been heavily criticized and excluded from consideration in the ESA evaluation (see references in USFWS 2010). Van Riper et al. (2014) produced climate-niche modeling results indicating *G. morafkai* is unlikely to be affected by regional effects of global warming, and is even predicted – an unlikely scenario – to increase in some of the most arid parts of its range in Arizona, where it is currently rare. Other ongoing modeling

efforts (Nussear, pers. comm., unpublished) point toward possible climate change-related decline in *G. morafkai*, but perhaps only under worst-case scenarios, while Sinervo (2014) reported that a physiologically based model with rising temperature projects catastrophic declines in desert tortoises essentially throughout their current geographic distributions.

This and other chapters in this report focus on evaluating the significance and implications of a growing set of field observations and census reports of large-scale and episodic mortality in desert tortoises in Arizona and Sonora, that seem related to drought (Wirt 1988, 1995; Wirt and Holm 1997a&b; citations in Appendix 1; Chapters 2-4), during a period of rapidly rising ambient temperatures since the 1960s apparently caused by greenhouse gas emissions (Garfin et al. 2013). In order to evaluate the climate threat to *G. morafkai* in Mexico, these chapters bring together a diverse set of mortality observations in the form of tortoise carcasses found in numerous localities, long-term repeat-census plot results, and climatic data related to widespread, climate-related populations reductions in *G. morafkai* throughout much of its geographic distribution. In this chapter the focus is on data from the repeat-census plots and their context within the summarized observations of *G. morafkai* mortality episodes across its entire distribution.

5.2 Methods

I assembled data from fieldwork, personal communications, and published reports on mortality events recorded as carcasses found in the wild for tortoises currently recognized as *G. morafkai*, including the genetically divergent populations in tropical thornscrub and tropical deciduous forest (Edwards et al., *submitted*) in northwestern Mexico. The largest body of this data were extracted from fieldwork reports on intensive study plots, censused from 1987 to 2008 (plus one in 2010), that were established in Arizona by Bureau of Land Management and Arizona Game and Fish Department (citations in Appendix 1). I did not have the original individual-based data on marks, sizes, locations, and exact capture dates but extracted information from published reports cited in Appendix 1. Study plot locations and other localities in Arizona from which data are reported here are shown in Fig. 5.1.

I summarized Arizona study plot data in four ways: (1) I extracted total individual live animals captured (*TOT_LIVE*) during each survey, separated into sexable adults and subadults (*TOT_AD*; those ≥ 180 mm mid-dorsal carapace length [MCL]) and unsexed juveniles (*TOT_JUV*; including all hatchlings, juveniles, and immatures); (2) I totaled all animals found dead in each survey (*TOT_DEAD*), and transcribed the published estimated year of death given in the report tables into a data table for analysis; (3) I copied all Lincoln-Peterson (L-P) population estimates for adults plus subadults (*POP_EST*) published in the reports, then reviewed the methods described and the data displayed for each one according to a set of rules (described in section 4.2.1) and either accepted or rejected it for further use; and (4) I examined all size-frequency histograms, mortality descriptions, and discussions of field observations relevant to plot populations' status, trends, and ecology connected to population regulation.

A previous attempt to summarize the Arizona study plot data (1987-2006) by Boarman and Kristan (2008) was criticized from several quarters (USFWS 2010 and therein). In part to avoid a repeat of this, I performed key statistical tests on the raw data (*TOT_LIVE*, *TOT_DEAD*, and *TOT_AD*) as well as *POP_EST*. There are,

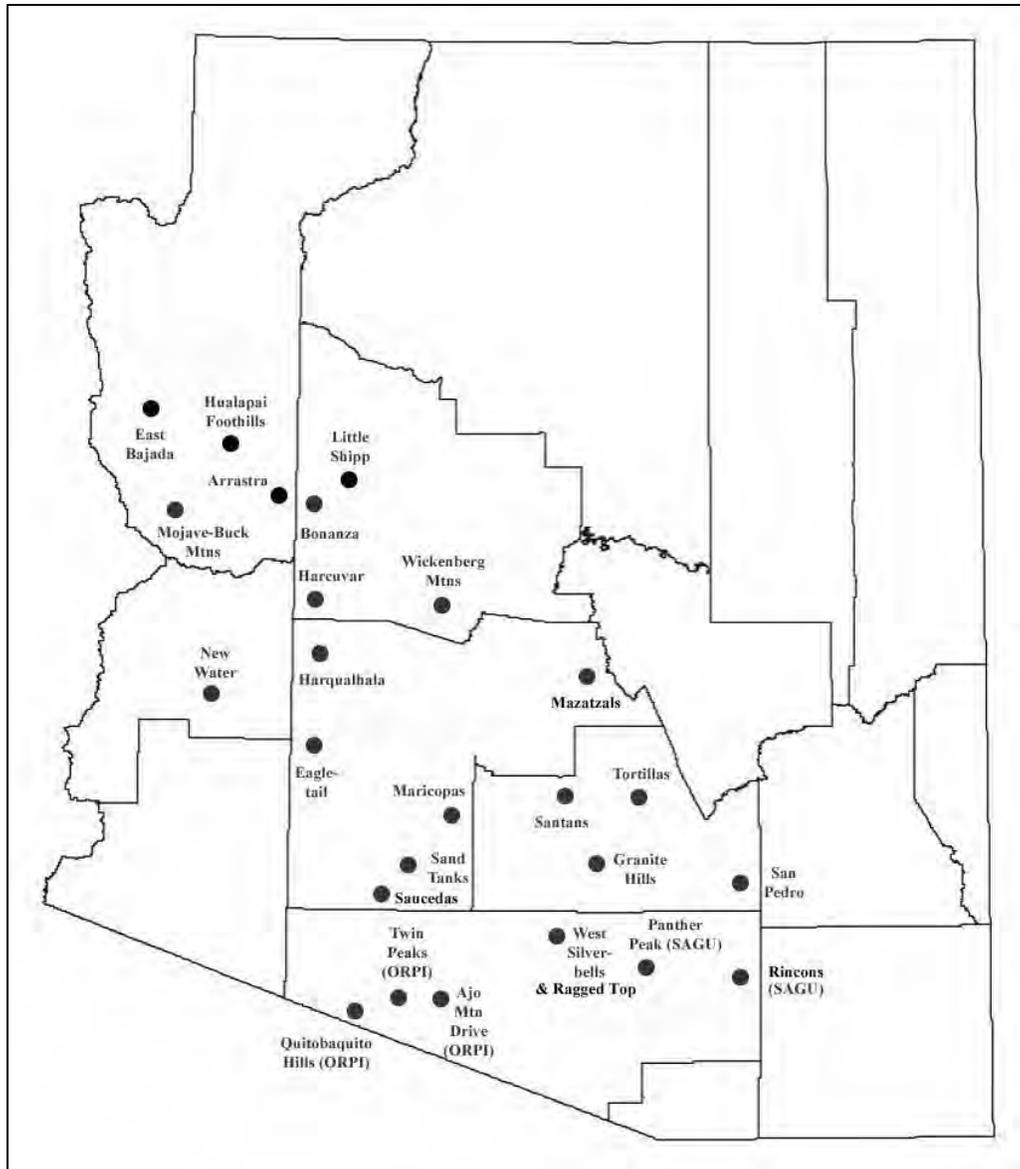


Figure 5.1. Study areas in Arizona mentioned in text, tables, and appendices.

however, stronger biases in the raw data than in the computed *POP_EST*. For example, population size calculations can yield a positive bias if undetected recruitment and immigration enters the sample recapture proportion used to compute the sampling proportion during the “marking” period. Since the sampling methodology varied over time to some extent during 1987-1999, and was altered in 2000 (Averill-Murray and Klug 2000), slight bias toward high estimates likely exists. Based on my calculations (where such were possible; see below), the high recapture proportions achieved, and the care taken by the report preparers, this bias over time appears to be small relative to the trends discussed herein. The trends seen in *POP_EST* mirrored those in *TOT_AD* but fluctuated less erratically – as expected from the remarkable recapture rates achieved and changes in field survey patterns; around 2000, fieldworkers were instructed to avoid surveying habitat that was apparently unsuitable and where no or very few tortoise encounters were previously made. Since they only focused on suitable habitat, the increased

time available resulted in more passes across the plots each census year, thus enhancing recapture rates. This means the total sample of individuals registered would rise as a result, as hard-to-find individuals were added to the total. Therefore, there would tend to be a bias toward relative over-estimation of populations later in the study period, especially for *TOT_LIVE* and *TOT_AD*, but also for *POP_EST*. These biases would tend to offset the biases described below that originated in use of inter-year sampling for *POP_EST* earlier in the study. Although crude, the L-P estimates tend to reduce the temporal bias in sampling pattern and intensity, and for that reason I emphasize *POP_EST* rather than *TOT_AD* in the presentation.

Criticism leveled at Boarman and Kristan (2008) came in several forms, which I have here attempted to circumvent by clearly defining and explaining the data used, computations, assumptions, justifications, and limitations of the analytic results. However, I acknowledge that Boarman and Kristan's (2008) computed estimates are likely the best available, and are not inconsistent with those I arrived at here according to the following criteria.

5.2.1 Abundance and Mortality

The rules I used for accepting *POP_EST* from the study plot reports were as follows:

- All intra-year computations were accepted, when based on two or more sampling periods (a "marking period" and one or more "recapture periods"), even if these methods were only specified for the year in question in later reports, or clearly implied.
- I accepted *POP_EST* if it was based on using recapture rates of adults plus subadults in one year applied to the number of the same cohort from the previous year. However, I applied these estimates as population size for the previous year (the "marking year"), not, as reported, to the year during which re-survey recaptures (the "recapture years") were obtained. The marking year is the population being estimated by this method, not the recapture year. I inspected the size-frequency histograms and rejected *POP_EST* if individuals at the size-class adjoining subadult were present in marking year, since the adult + subadult cohort in the recapture year could not be exclusively identified among the sample in the marking year.
- I rejected estimates made using marking year up to 2-4 years before recapture year, except where it was evident from age structure that recruitment of always-undersampled, smaller, younger individuals into the subadult size class would have been rare or absent by recapture year. In practice, this was only possible when there were no observations in the immature 1 and 2 age-size classes in the marking year.
- In three cases, using reported size distributions and adequately specified recapture histories, I computed modified Lincoln-Peterson estimates for adjoining or nearly adjoining survey years for the 1987-1999 period. Also, for early surveys in the record, I checked on similar computations from the reports. When adequately described capture histories were available, I used my estimates from the reported, data, which were similar to but slightly lower than those published, as I more carefully parsed the age-size structures for L-P estimate computation.

- In one case where no *POP_EST* was presented, I equated *POP_EST* with the total sample of individuals (adults + subadults) based on statements in the report detailing a long series of many recaptures without new individuals during approximately the second half of the survey.
- For middle to late surveys (2000 – 2010), I accepted the computations presented in the reports, as these were more consistently sound in relation to the desired comparisons to earlier years in this record.

I refer to these population size estimates as “abundance” rather than density because none of them were computed explicitly with respect to movement dynamics across plot boundaries; thus, effective areas sampled have not been prepared. Inter-year methods for computing abundance will produce biases on the high side, compared to intra-year estimation methods, based on the reasonable assumption that recapture rate dilution by movement of previously unsampled individuals into the plot would be greater after longer time periods. For inter-year data at Panther Peak, estimates were higher than intra-year estimates by about 10-15 %, presumably due to movement across plot perimeter effects (P. Holm, pers. comm.). However, the perimeter:area ratio for 1 km² plots such as Panther Peak (4.0 km/km²) is greater than that for the 2.56 square km plots (1.56 km/km²) for which this problem occurs in the dataset. This suggests the bias may be ≈5% or less. Home ranges of tortoises are generally small (4-20 ha) compared to the plot dimensions (256 ha [1 mi²] in most cases) and tortoises tend to be philopatric over time (Averill-Murray and Klug 2000; Averill-Murray et al. 2002). This was further indicated by consistency of the estimate sequences (including those I excluded), as described in Results. Finally, estimated apparent annual survivorship (= 1 – mortality – emigration) for adults and subadults in this dataset was 0.93 (Zylstra et al. 2012), which is highly unlikely to be more than 4% lower than true survivorship, implying that immigration and emigration rates from the plots are not large. Therefore, I ignored the bias problem, except that in the Discussion I interpret small or medium-sized declines from the early estimates in the record with caution and focus on the larger mortality events. I note that the original data are likely well suited for analysis of abundance, density, and several demographic parameters using methods of Royle and Dorzio (2008).

With these data in hand, I computed the following proportions of year samples at individual sites:

$$MORT \text{ (mortality intensity)} = TOT_DEAD / (TOT_LIVE + TOT_DEAD) \quad (1)$$

$$RECRUIT \text{ (juvenile relative abundance)} = TOT_JUV / TOT_LIVE \quad (2)$$

I chose not to refine juvenile relative abundance or focus on it in depth in this analysis because I had no population-specific growth data or growth-ring based age structures with which to parse recruitment in a more useful way. Because juvenile growth and recruitment into the subadult and adult population are slow, it was possible to conduct the mortality analysis presented here despite the insufficiency of the recruitment analysis.

It was not possible to compute population change for successive years, as the few plots censused in successive years were done when and where population changes were minor. I therefore computed mean *POP_EST* for the 1987-1998 period and for the 2000-2010 period, and used the proportional change:

$$\ln (\Delta POP_EST_{decadal}) = \ln (POP_EST_{1987-1998}) - \ln (POP_EST_{2000-2010}) \quad (3)$$

as an index for the trend at each site. I chose these two aggregate periods, for which site means were computed for each period, to capture large-scale changes between clusters of early and late censuses in the study record, and also computed arithmetic mean *MORT* and *RECRUIT* for each site during each period.

I analyzed abundance as a function of time (*YEAR*) using AICc, BICc, and r^2 in both total *TOT_AD* and *POP_EST* and compared general linear models for temporal change in *POP_EST*:

$$TOT_AD \sim YEAR \quad (4)$$

$$POP_EST \sim YEAR, SITE, SITE*YEAR \quad (5)$$

To evaluate demographic effects on population decline, I compared general linear models for abundance:

$$TOT_AD \sim MORT, RECRUIT, SITE \quad (6)$$

$$POP_EST \sim MORT, RECRUIT, SITE \quad (7)$$

And:

$$\Delta POP_EST_{decadal} \sim MORT_{decadal} + RECRUIT_{decadal} \quad (8)$$

5.2.2 Estimated Year-Specific Mortality and Population Declines

I extracted all the estimated year-of-death data from the plot reports of tortoise carcasses found in the field. I assigned year-of-death based on these data, as follows:

- Year of death assigned precisely (“dead < 1 yr”): I accepted as-is.
- Range of 2-years (“dead 1-2 yr”): I split number equally between years
- Range of three years (“dead 2-4 years”): split number equally among the three years
- Older (“dead > 4 years): split equally among years 5-7.

For the Maricopa Mountains study plot, I used year-of-death assignments from Wirt (1995) and Wirt and Holm (1995, 1997), who provided a more rigorous accounting through 1995.

From these criteria I tabulated the carcass-based mortality values for each year for a total number of observed mortalities per each year for each plot, $MORT_{YR, PLOT}$. From these I derived an aggregate estimate of average number of mortalities observed each year, $MORT_{YR}$, over all census plots for which carcasses were ascribed to a year based on the field data and the criteria listed above, yielding:

$$MORT_{YR} = \sum MORT_{YR, PLOT} / \sum PLOTS \quad (9)$$

This result is sensitive to the varying intervals and number of times plots were censused over the 1987-2010 timespan; I therefore applied a correction factor equal to the 5-year running mean of number of plots worked. This correction factor is imperfect but is the best available. I chose 5 years as the time span over which some specification of time-since-death is presumed to be available. This could not be applied to 2008 and 2010 (which had few or no following census years, and were outliers that were deleted from further analysis). From $MORT_{YR}$, I computed an aggregate annual mortality fraction for the census plot data:

$$\% MORT_{YR i} = MORT_{YR i} / POP_EST_{YR i}, \quad (10)$$

where i and $i-1$ represent any successive years, and the denominator derived from the analysis of Eq. 7.

5.2.3 Mortality and Drought Patterns

The result for $\% MORT_{YR i}$ is the most unbiased estimate of annual mortality rate available from the published carcass data. Not all carcasses of tortoises that died were found, so $\% MORT_{YR i}$ underestimates annual mortality and is an index value. I computed regressions for $\% MORT_{YR i}$ as functions of annual values for total precipitation (*PRECIP*), Palmer Drought Severity Index (*PDSI*), and mean air temperature (T_a) using the average climate values over the six National Climate Information Center divisions of Arizona in which tortoises occur and were studied on census plots. These regressions were computed using 5 time-lag values (0-4 years) and two- and three-year running means of climate values. Time did not permit likely informative evaluations of local climate data from near each plot.

The population data used in this study are in Appendix 1. I examined scatter plots, residuals, and data histograms to ensure there were no gross violations of normality assumptions underlying the general linear models. Natural log transformed abundance values were close to normal. However, as mortality data were skewed, I checked significance levels on ranked abundance and mortality: these tests all supported the statistical significance indicated for the parametric statistics, which are presented herein. I evaluated linear models by selecting those with the lowest AICc and BICc. To estimate the level of *MORT* in this dataset on *POP_EST* I performed a step-wise data-deletion bootstrap by progressively eliminating the largest mortality event and then using $P \leq 0.05$ (1-tailed) to identify observed carcass sample fractions that may index recent population declines. Computations were done in Microsoft Excel and SAS JMP.

5.3 Results

5.3.1 Demographic and Mortality Observations

Trends of estimated population, sample fractions of juveniles, and carcasses of *G. morafkai* on Arizona study plots are shown and annotated in Figs. 5.2 – 5.9. Major population reductions ($\geq 60\%$) occurred in 4 of 17 study populations (Figs. 5.2 and 5.3): observations of carcasses indicate that these reductions occurred in 1987-1990 (1 case) and prior to the end of 2002 (3 cases). A fifth population, which was only studied from 2002-2010, also showed a substantial proportional decline (Fig. 5.3). Four additional study populations showed reductions in estimated population associated with episodes of elevated mortality (Figs. 5.4 and 5.5). Six relatively large populations in diverse settings displayed limited or no evidence of reduction, and large numbers of dead tortoises were not found in any of them (Figs. 5.6 and 5.7). Two smaller populations also displayed evidence for neither marked reduction nor elevated mortality episodes, and one, in a relatively arid region, may have increased during the duration of observation (Figs. 5.8 and 5.9). The proportion of juveniles in these study populations was not obviously associated with trends in estimated population, although the graphics suggest that elevated recruitment was associated with relative population stability in three or four cases (Fig. 5.4, Bonanza Wash; Fig. 5.5, Eagletail Mountains; Fig. 5.6, Granite Hills and Little Shipp Wash).

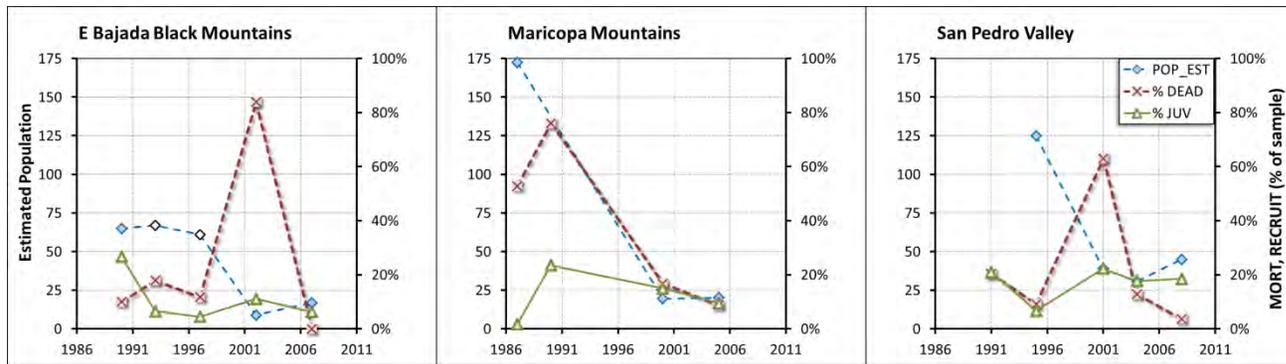


Figure 5.2. Decimated populations with catastrophic mortality episodes in late 1980's and early 2000's. East Bajada is in northwestern portion of species range; Maricopa site is at relatively low elevation in Lower Colorado Valley margin; San Pedro site is at relatively high elevation near eastern range margin. Open black diamonds are estimates not used for analysis.

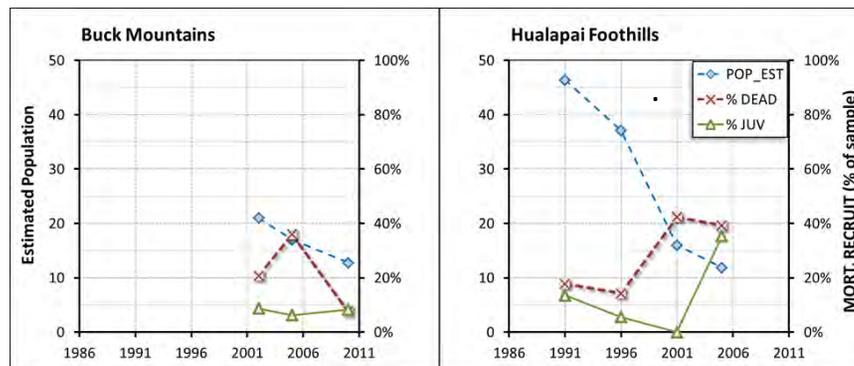


Figure 5.3. Declining populations at moderate (core) elevations in northwestern portion of range, associated with elevated mortality in early 2000's.

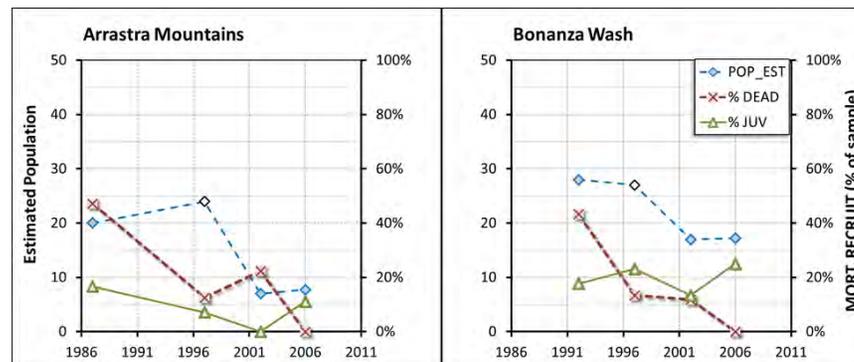


Figure 5.4. Small populations at relatively high elevation near the species' northern range limit, with evidence suggesting preceding mortality episodes in late 1980's and possibly early 1990's.

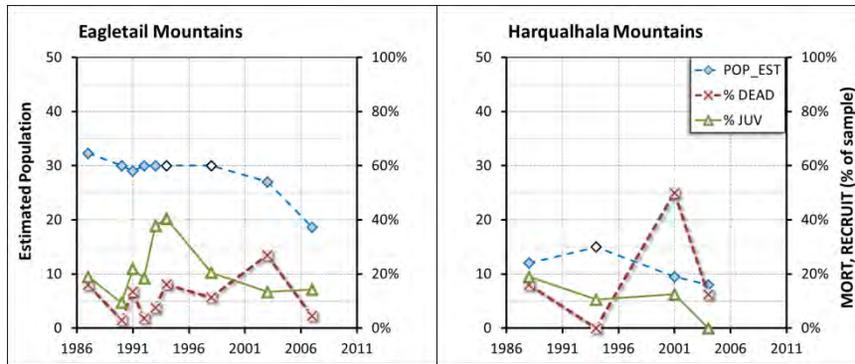


Figure 5.5. Small populations, near northwestern core of the species' range, with evidence suggesting possible recent, moderate declines associated with elevated mortality. Eagletail Mountains study population, at moderate-low elevation in the margin of the Lower Colorado River Valley, may be supported by consistent recruitment. Harquahala Mountains study population, at moderate-high elevation in the margin of the Arizona Upland, may have had a significant mortality episode in the late 1990's or early 2000's

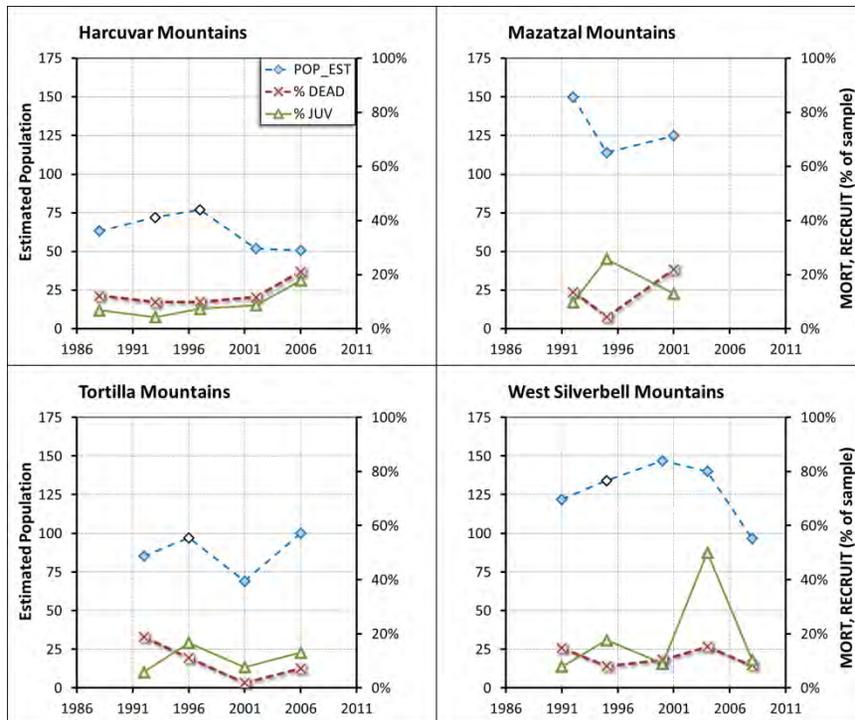


Figure 5.6. High abundance, relatively stable populations, at moderate elevations in core of species range, with low mortality and moderate recruitment.

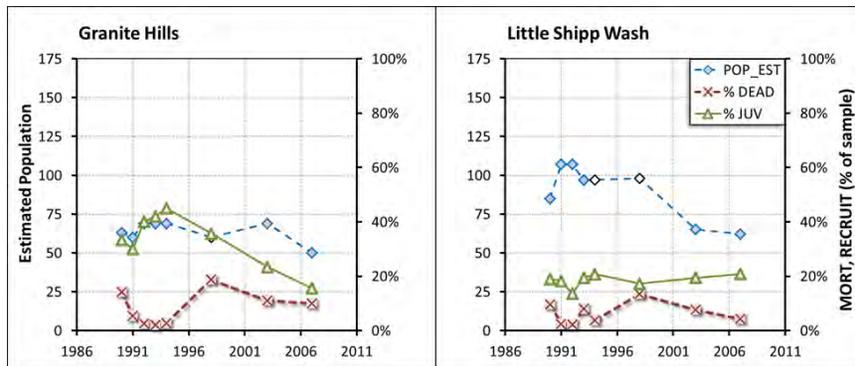


Figure 5.7. High abundance, relatively stable populations with high recruitment and moderate mortality. Granite Hills study population, in the Arizona Upland margin at moderate elevation, may be declining with recently decreasing recruitment. Little Shipp Wash site is at moderate-high elevation near northern range limit or the species; Schneider (1981) found 33.1% juveniles in a 1980 sample of 51 tortoise at this site; population decline may be occurring.

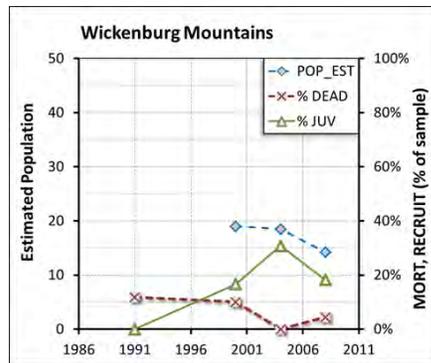


Figure 5.8. Small population of uncertain status, at relatively high elevation near northern range margin of species, with indication suggesting recent recruitment in progress.

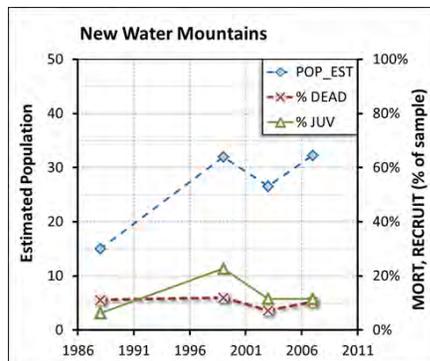


Figure 5.9. Apparently increasing small population, at relatively low elevation in Lower Colorado River Valley margin, with moderate recruitment and low mortality.

Table 5.1. Mortality episodes in *Gopherus morafkai* populations in Arizona, USA and Sonora, Mex., 1985-2013. "Timing" is when observations occurred; mortality timing, if different, is under "Mortality Observed".

Timing	Location	Mortality Observed	Estimated Effect	Data Source
1985-6	Waterman Mts., AZ	Ca. 12 intact shells (died \approx 1981-1984), local bajada area	unknown	Clay May (pers. comm. 2014)
1987	Maricopa Mts., AZ	mass mortality	ca. 85% persistent decline in estimated population	AGFD-BLM plot results
1987	central Sonora	widespread mortality	"fewer tortoises" reported by local people	Trevino et al. 1991
1987	Arrastra Mountain, AZ	high number and proportion of carcasses in plot survey	unknown; possible decline in progress	AGFD-BLM plot results
1987	Bonanza Wash, AZ	high number and proportion of carcasses in plot survey	unknown; possible decline in progress	AGFD-BLM plot results
1987-1991	Organ Pipe Cactus NM, AZ	high proportion dead in surveys	unknown	Chapter 4
1987-1991	Sand Tank and Saucedo mts., AZ	mass mortality, low abundance on transects and 6 plots	104 carcasses, few live tortoises	Wirt and Holm 1997; Dames and Moore 1994; Geo-Marine 1994
1996	Ragged Top - upper bajada (east), AZ	mass mortality (8+ found dead in population of 7-22)	ca. 75+% local population decline; 1 known survivor	Repp, in Rosen (2003)
1998-2003	Granite Hills, AZ	moderate no. of carcasses in population with high abundance and % juveniles	no decline or slight decline	AGFD-BLM plot results
1999-2001	San Pedro Valley, AZ	mass mortality	ca. 70 % decline with possible slight recovery	AGFD-BLM plot results
2000-2001	Sells region, AZ	14 dead, 7 live: \approx 8 died 1999-2000, including 8 at one sites	unknown	Rosen et al. 2002
2002	Tiburón region, Sonora	20 dead <2 yr , 22 dead 2-4 yr, 7 dead > 4 yr; 29 live	decline shown for Tiburón plot (Caracól)	Chapter 3
2002	Eastern Bajada, Black Mts, AZ	mass mortality	ca. 66+% persistent decline in estimated population	AGFD-BLM plot results
2003	Eagletail Mts, AZ	moderately high number of carcasses found in plot survey	ca. 40% decline in estimated population	AGFD-BLM plot results
2001-2005	Hualapai Mts. Foothills, AZ	moderate numbers of carcasses; most died 2000-2004	ca. 70% reduction in estimated population	AGFD-BLM plot results
2005	Buck Mts, AZ	high number and proportion of carcasses in plot survey	ca. 50% reduction in estimated population	AGFD-BLM plot results
2010-2011	SSW of Caborca, Sonora	8 found during 2012 sampling; 7 died in \approx 2011 or 2010	unknown	Chapter 2
2005-7, 2013	NE of Obregon, Sonora	high proportion of carcasses in surveys in thornscrub	unknown	Chapter 2

Table 5.1 lists nine instances of mortality episodes from the census plots (Figs. 5.2 – 5.4 and 5.5, part and 5.6, part) with ten other observed mortality episodes of *G. morafkai* populations in Arizona and Sonora in local regions or study areas. A possible additional case on the Arizona census plots was in a very low-density site (Harquahala Mountains, Fig. 5.5) but sample size is small. An additional case on Isla Tiburón, Sonora, involved a formal plot survey indicating a major population reduction (Chapter 3), which was associated with drought (Hallack-Alegria and Watkins 2007; Stahle et al. 2009). In four additional observed episodes, mortality was reported to involve abundance reductions or was so severe that reductions can be assumed (Organ Pipe Cactus National Monument, AZ; Ragged Top, Ironwood Forest National Monument, AZ, Sand Tank and Saucedo mountains, AZ). Known mortality episodes are widespread, occurring in most of the species' range and spanning a period of four decades. Periods of regional drought in the Sonoran Desert region are associated with most of these episodes (late 1980s, 1996-1997, 2000-2002, mid 2000s, 2011-2013).

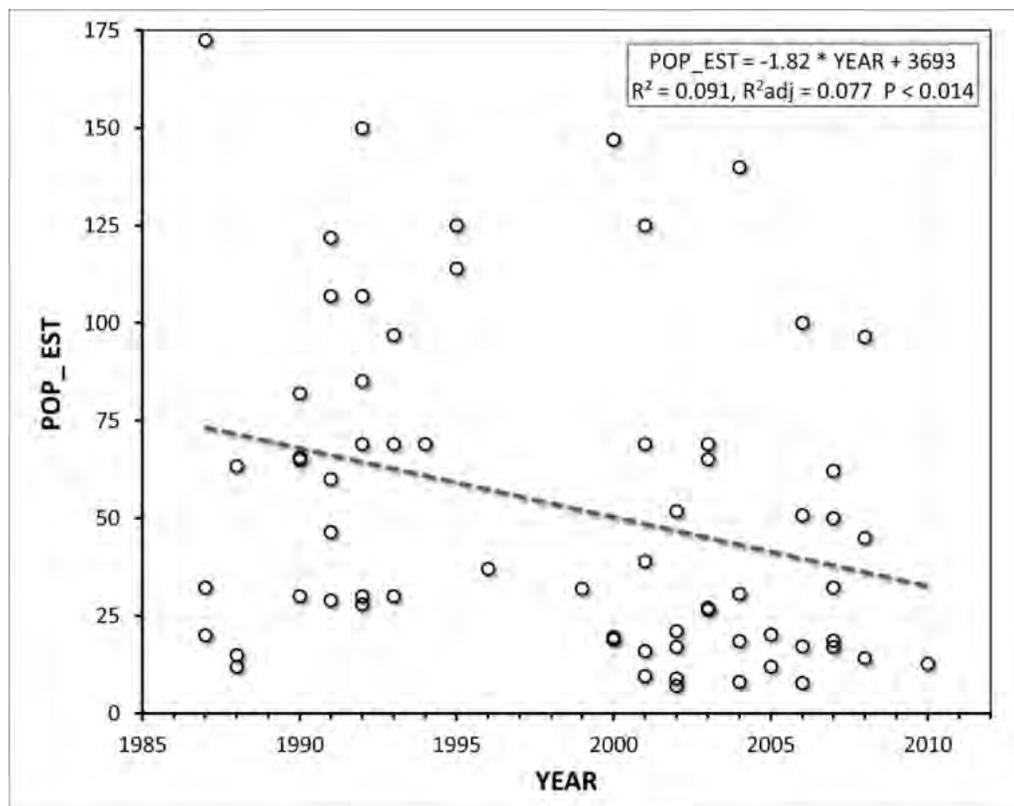


Figure 5.10. Population estimates for *Gopherus morafkai* from 17 repeat-census plots (citations in Appendix 1) that were used in this analysis.

5.3.2 Population Change and Demographics

The number of adult plus subadult tortoises found per plot census decreased significantly over the duration of study ($TOT_AD = 1574 - 0.770 * YEAR$, $P < 0.04$), as did estimated abundance (best models: $POP_EST = 3414 - 1.68 * YEAR + SITE$ and $POP_EST = 3638 - 1.79 * YEAR + SITE + (SITE*YEAR)$, $P(YEAR) < 0.0003$; see Fig. 5.10). The preferred model for POP_EST , based on BICc, included $SITE*YEAR$ interaction term, which is biologically more reasonable than the model without the interaction term, despite the

slightly lower AICc for the latter (Table 5.2). These regressions display ≈50% reduction in abundance over 23 years.

The best models relating demographics to change in tortoise populations both included strongly significant effects for mortality ($P < 0.0001$). A model including only mortality had the lowest BICc

$$(\ln(\Delta POP_EST) = 0.0676 - 1.871 * MORT),$$

while a model with both mortality and recruitment ($\ln(\Delta POP_EST) = -0.010 - 1.820 * MORT - 0.400 * RECRUIT$) had a slightly lower AICc but was of questionable realism with the recruitment variable having a negative effect on population increase. Similar

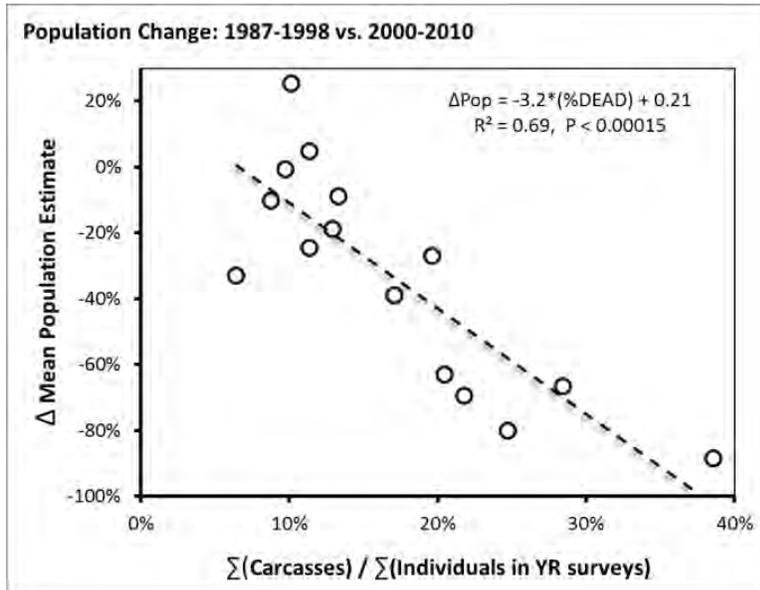


Figure 5.12. Decadal change in abundance and mortality.

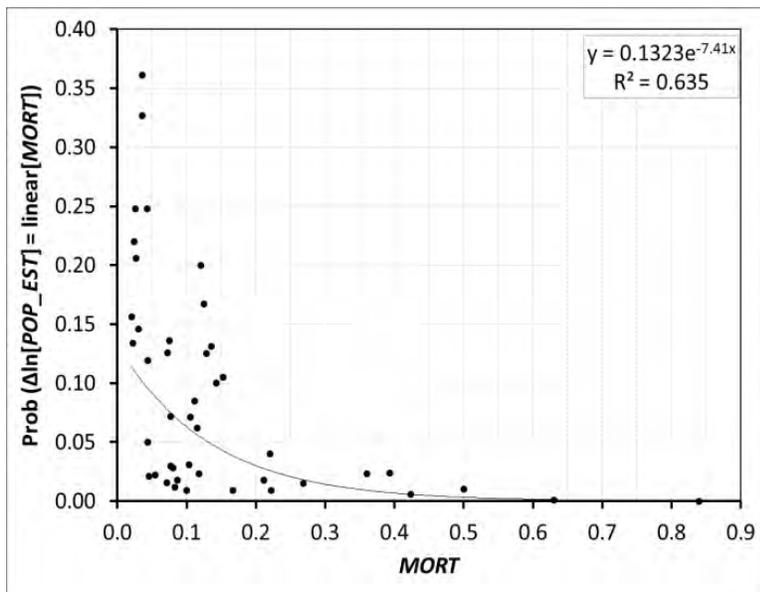


Figure 5.11. Stepwise data-deletion bootstrap for P-value.

results occurred when tortoise abundance was indexed by the number of adults plus subadults recorded in each census ($\ln(\Delta TOT_AD)$; see Table 5.2).

The best demographic model for decadal change in abundance included only mortality ($\Delta POP_EST_{decadal} = 0.212 - 3.211 * MORT$; $P <$

0.0001) and indicates a strong effect (Fig. 5.11), indicating that observations of large numbers and high proportions of carcasses may signal population declines. Removing the populations with the five greatest reductions in $\Delta POP_EST_{decadal}$ extinguished statistical significance ($P > 0.1$, 1-tailed), as did eliminating the top 11 declines in ΔPOP_EST computed for individual sites using adjoining estimates. Step-wise data-deletion bootstrap indicated that carcass fraction of $> 20\%$ of total sample, and possibly

as low as 12 % in samples comparable to those from the census plots were associated with population reductions (Fig. 5.12).

5.3.3 Observed Mortality and Climate

The temporal distribution of estimated year-of-death for carcasses reported on the repeat-census study plots and estimated mortality rates derived from it are shown in Fig. 5.13. Peaks of mortality are indicated for dry times (1987-1990; 1996-1997, 2000-2003, and toward the end of the study period; Fig. 5.14). These peaks preceded the most severe years of drought: examination of details of the field data (Appendix 1) indicate that, at least for some of the largest declines, major surges in discovered carcasses did actually precede the most severe period of individual droughts.

The top two models ($\Delta AICc < 0.5$) included precipitation, with two-year running mean precipitation slightly better than precipitation in the year mortality was estimated to have occurred. Other models with lower AICc but for which regression coefficient was significant included PDSI in year of mortality, PDSI two-year running mean, precipitation three-year running mean, and mean annual temperature two-year running mean (see Table 5.3).

5.4 Discussion

5.4.1 Overview and Caveats

The analysis here of the census plot data for *Gopherus morafkai* in Arizona demonstrates that mortality observations, in the form of carcasses found during census work on 17 study areas located in good habitat throughout the regional distribution, are associated with a substantial decline of the species, which approximates a 50% reduction in abundance from 1987 to 2010. The estimated decline is similar to findings presented by Boarman and Kristan (2008) that received criticism (USFWS 2010 and therein), and the correlation of mortality with estimated population declines negates suggestions that the declines are artifacts of estimation methods. Suggestions that observed episodic mortality events and population reductions in *G. morafkai* are isolated events and thus not indicative of a major decline of the species (see USFWS 2010) are similarly negated by the analysis here and the summary of 19 observed mortality episodes (Table 5.1; and see Chapters 2-4).

There are caveats to consider for the magnitude of decline, related to methodological issues described in the Methods section. The use of inter-year recaptures early in the study tends to inflate abundance estimates. However, more thorough sampling of actual (i.e., utilized) habitat late in the study, which would have resulted in higher fractions of the populations being registered, tends to raise estimates as less detectable individuals become better represented in the computations. These important biases are balancing, with respect to looking at trends from early to late in the study. The relatively sedentary and philopatric spatial ecology of the species, and the effective census methods ($\geq 60\%$ of adults and subadults registered most censuses), will limit the size of these two biases. Although additional analysis of the original data using hierarchical modeling (Royle and Dorzio 2005) will be required to obtain more refined and certain abundance estimates, the magnitude of reductions in estimated abundance and the

Table 5.2. Models tested relating Sonoran Desert tortoise abundance in relation to time and demographics.

dependent	predictor	equation	R^2	R^2_{adj}	P -values	AICc	BICc	Δ AICc	Δ BICc
TOT_AD	YEAR	1574 - 0.770 * YEAR	0.05	0.04	0.036	764.4	771.4	na	na
POP_EST	YEAR, SITE	3414 - 1.68 * YEAR + SITE	0.80	0.73	0.0003 (YEAR), <0.0001 (SITE)	626.3	651.3	0.00	13.58
POP_EST	YEAR, SITE, YEAR*SITE	3638 - 1.79 * YEAR + SITE + (SITE*YEAR)	0.94	0.88	<0.0001 (YEAR), <0.0001 (SITE), <0.0001 (SITE*YEAR)	645.1	637.8	18.86	0.00
POP_EST	YEAR	3693 - 1.821 * YEAR	0.09	0.08	0.014	679.2	685.4	52.90	34.00
ln(POP_EST)	YEAR, SITE	79.54 - 0.038 * YEAR + SITE	0.86	0.81	<0.0001	89.8	111.4	0.00	7.80
ln(POP_EST)	YEAR, SITE, YEAR*SITE	86.02 - 0.041 * YEAR + SITE + (SITE*YEAR)	0.96	0.91	0.0005 (YEAR), <0.0001 (SITE), 0.0008 (SITE*YEAR)	130.6	103.6	40.80	0.00
ln(POP_EST)	YEAR	89.92 - 0.0432 * YEAR	0.09	0.08	0.009	154.9	160.8	65.10	49.40
ln(TOT_AD)	YEAR	61.20 - 0.0290 * YEAR	0.07	0.06	0.014	179.7	186.7	89.90	75.30
ln(Δ TOT_AD)	MORT, RECRUIT	0.328 - 2.202 * MORT - 0.579 * RECRUIT	0.63	0.62	<0.0001 (MORT), 0.086 (RECRUIT)	39.7	47.8	0.00	1.10
ln(Δ TOT_AD)	MORT	0.227 - 2.221 * MORT	0.62	0.61	<0.0001	40.5	46.7	0.80	0.00
ln(Δ TOT_AD)	MORT, RECRUIT, SITE	0.376 - 2.369 * MORT - 0.708 * RECRUIT + SITE	0.68	0.55	<0.0001 (MORT), 0.185 (RECRUIT), >0.5 (SITE)	85.3	110.3	45.60	62.50
ln(Δ POP_EST)	MORT	0.0676 - 1.871 * MORT	0.37	0.35	<0.0001	58.2	63.3	0.00	0.00
ln(Δ POP_EST)	MORT, RECRUIT	-0.010 - 1.82 * MORT + 0.400 * RECRUIT	0.38	0.35	<0.0001 (MORT), >0.4 (RECRUIT)	60.0	61.6	1.79	-1.72
ln(Δ POP_EST)	MORT, SITE	0.103 - 2.216 * MORT + SITE	0.59	0.36	<0.0001 (MORT), >0.4 (SITE)	95.0	104.7	36.83	41.38
ln(Δ POP_EST)	MORT, RECRUIT, SITE	-0.005 - 2.25 * MORT + 0.719 * RECRUIT + SITE	0.60	0.36	<0.0001 (MORT), >0.3 (RECRUIT), >0.4 (SITE)	99.1	106.9	40.93	43.58
Δ POP_EST _{decadal}	MORT	0.212 - 3.211 * MORT	0.69	0.67	<0.0001	0.461	0.518	0.00	0.00
Δ POP_EST _{decadal}	MORT, RECRUIT	0.328 - 3.366 * MORT - 0.583 * RECRUIT	0.70	0.65	<0.0001 (MORT), >0.5 (RECRUIT)	2.938	1.770	2.48	1.25

Table 5.3. Models tested for *Gopherus morafkai* mortality in relation to climatic parameters.

dependent	predictor - time lag	intercept	coefficient	R^2	R^2 adj	P-value	AICc	BICc	Δ AICc	Δ BICc
$\ln (\% MORT_{YR\ i})$	Precip _{2-YR} running mean	1.833	-0.0695	0.295	0.258	0.011	12.48	14.20	0.00	0.00
$\ln (\% MORT_{YR\ i})$	Precip ₀	1.650	-0.0550	0.280	0.243	0.014	12.92	14.64	0.44	0.44
$\ln (\% MORT_{YR\ i})$	PDSI ₀	0.913	-0.0655	0.215	0.174	0.034	14.74	16.46	2.26	2.26
$\ln (\% MORT_{YR\ i})$	Precip _{3-YR} running mean	1.862	-0.0712	0.214	0.172	0.035	14.78	16.50	2.30	2.30
$\ln (\% MORT_{YR\ i})$	PDSI _{2-YR} running mean	0.907	-0.0808	0.197	0.154	0.044	15.23	16.95	2.75	2.75
$\ln (\% MORT_{YR\ i})$	T _{2-YR} running mean	-12.774	0.2126	0.196	0.154	0.045	15.25	16.97	2.77	2.77
$\ln (\% MORT_{YR\ i})$	T ₀	-9.528	0.1623	0.175	0.131	0.059	15.79	17.52	3.32	3.32
$\ln (\% MORT_{YR\ i})$	T _{3-YR} running mean	-12.193	0.2037	0.128	0.082	0.111	16.95	18.67	4.47	4.47
$\ln (\% MORT_{YR\ i})$	Precip ₁	1.493	-0.0367	0.125	0.079	0.116	17.03	18.75	4.55	4.55
$\ln (\% MORT_{YR\ i})$	T ₁	-6.997	0.1233	0.094	0.047	0.175	17.75	19.47	5.27	5.27
$\ln (\% MORT_{YR\ i})$	PDSI _{3-YR} running mean	0.928	-0.0649	0.086	0.038	0.197	17.94	19.66	5.46	5.46
$\ln (\% MORT_{YR\ i})$	PDSI ₁	0.949	-0.0334	0.053	0.003	0.316	18.69	20.41	6.21	6.21
$\ln (\% MORT_{YR\ i})$	PDSI ₂	0.981	0.0177	0.016	-0.036	0.588	19.50	21.22	7.02	7.02
$\ln (\% MORT_{YR\ i})$	Precip ₂	1.045	-0.0057	0.003	-0.050	0.920	19.77	21.49	7.29	7.29
$\ln (\% MORT_{YR\ i})$	T ₂	0.555	0.0065	0.000	-0.052	0.943	19.82	21.55	7.35	7.35

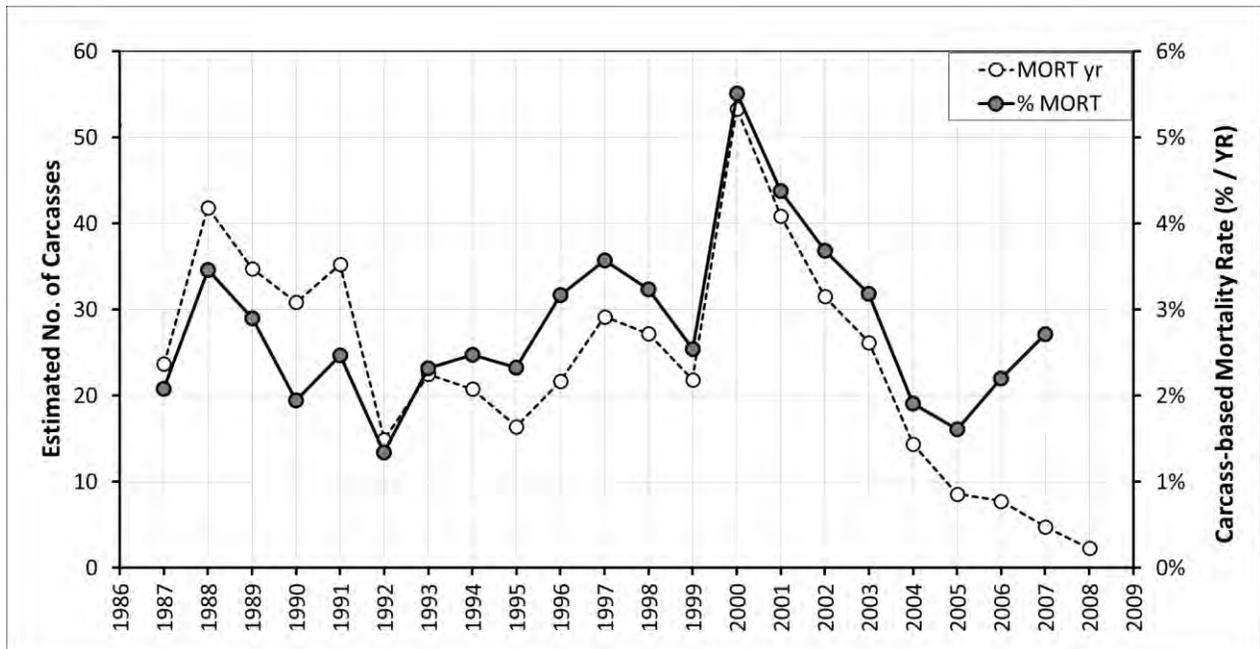


Figure 5.13. Carcasses of *Gopherus morafkai* from repeat-census assigned to estimated year-of-death, and indexed mortality rates (% MORT YR i) derived from the carcasses.

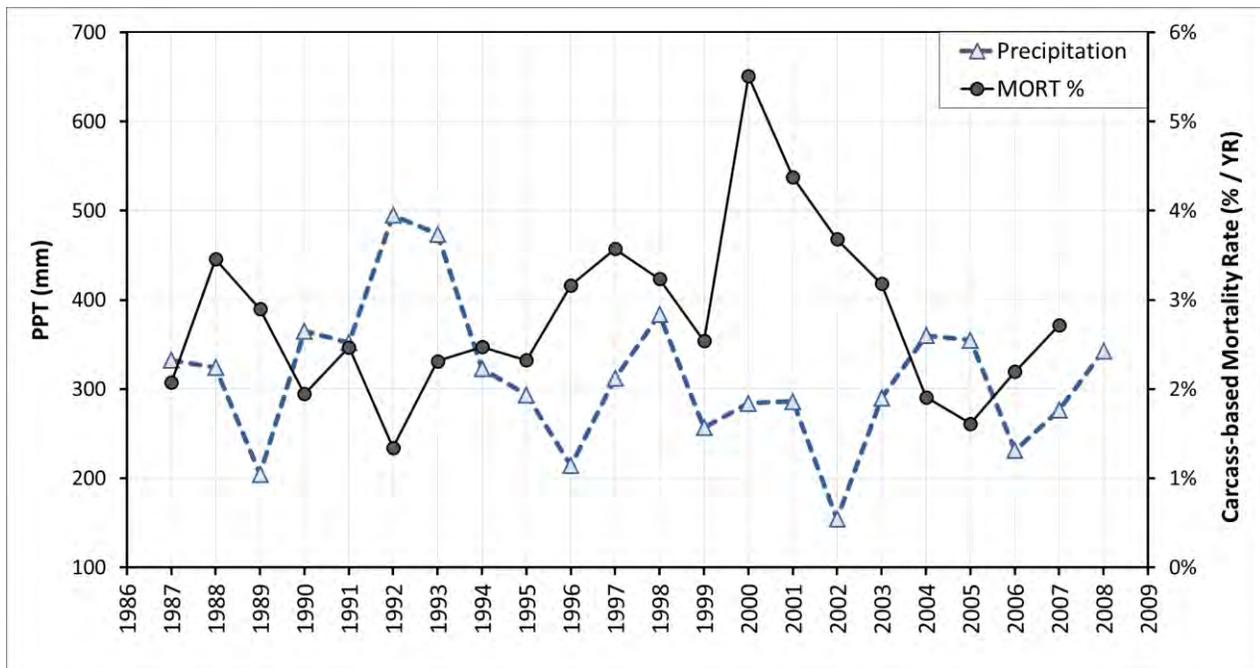


Figure 5.14. Mean values for indexed mortality rates (% MORT YR i) of *Gopherus morafkai* from 17 repeat-census study plots compared to temporal sequence of annual precipitation for the regions in which study plots were located.

strong relationship between observed mortality and abundance changes demonstrate that a significant decline has occurred across the combined area of the census plots.

The most pronounced and certain evidence demonstrating the decline is the major abundance reductions at five study plots (Maricopa Mountains, Isla Tiburón, Hualapai Mountains Foothills, San Pedro Valley, and Eastern Bajada of Black Mountains), associated in each case with large numbers of observed carcasses. A summary of observations throughout most of the species' distribution, in both the United States and Mexico, includes 19 known episodes of locally high mortality observations, 1985-2013, at least six of which involved >>20 % dead animals observed. The results presented here suggest that mortality fractions > 17-20% likely signify significant abundance reductions. These mortality episodes, which occurred during a 4-5 decade period of rising air temperatures, are associated with drought periods, which is consistent with key findings for adult and subadult survivorship on the Arizona census plots (Zylstra et al. 2012).

5.4.2 Geography of Population Status

The geography of population size and trend (Fig. 5.1; Table 5.1; Appendix 1) suggest a pattern. Declining and decimated populations are found peripheral to the core of the Sonoran desert tortoise ecological and geographic distribution: (1) In the margin of the arid Lower Colorado River Valley (LCV) subdivision of the Sonoran Desert during late 1980's (Maricopa, Sand Tank, and Saucedo mountains and Organ Pipe Cactus National Monument); (2) near the arid northwestern-most range in a region transitional between LCV and Mojave desertscrub (Eastern Bajada of Black Mountains, Buck Mountains, Hualapai Mountains); (3) near sea level in the Central Gulf Coast subdivision of the Sonoran Desert in coastal Sonora, Mexico (Tiburón Island, Seri Coast); (4) at or near the northeastern range margin at moderate-high elevation (San Pedro River Valley) and the northern range margin at relatively high elevations (Arrastra Mountains and Bonanza Wash); and (5) in south-central Sonora in relatively hot, low-elevation thornscrub near the southernmost end of the species' range, where genetic data show the Sonoran desert tortoise is transitional to a Sinaloan form of desert tortoise, which occurs to the east (at higher elevation) and south in mesic tropical thornscrub and tropical deciduous forest.

Relatively large populations in which large mortality episodes and population reductions have not been reported occur in a core geographic area and largely at moderate elevations within the species distribution in Arizona, principally within well-developed arborescent desert in the Arizona Upland subdivision of the Sonoran Desert. These sites are in the Harcuvar, Mazatzal, Rincon, Tortilla, Tucson, and West Silverbell mountains, nearby in the margin of the Arizona Upland at moderate elevation (Granite Hills), and at moderate-high elevation in the Arizona Upland near the northern range limit (Little Shipp Wash). Large populations were also observed in Sonora, Mexico during 2006-2013 (see Chapter 2) near Hermosillo in the Plains of Sonora subdivision of Sonoran Desert, northwest of Caborca in Arizona Upland, and southwest of Caborca in highly productive Lower Colorado River Valley Sonoran Desertscrub. Desert tortoises with Sinaloan genotypes (Edwards et al., *submitted*) are abundant in tropical deciduous forest at several localities in the Alamos region, where little mortality has been observed (Chapter 2).

Smaller populations that may be stable or recently declining in association with mortality episodes are found near the western core of the species' distribution in Arizona (Eagletail Mountains and Harquahala Mountains) and possibly at moderate-high elevation near the northern range margin (Wickenburg Mountains).

The most striking examples of persistence under arid conditions have been observed at two localities near the western range margin in the LCV: (1) at a census plot in New Water Mountains with a relatively small, but apparently increasing or stable population; and (2) in a large area around Sierra el Viejo southwest of Caborca, where tortoises are abundant on bajadas and in mid-valley xeroriparian environment (see Chapter 7).

5.4.3 Climate Change, Drought, and Conservation Status

Climate change projections (IPCC 2013) all predict, with very high confidence, continued, substantial rise in air temperatures in the range of *G. morafkai* through the 21st century. Most climate models also predict reduced winter-spring precipitation in the region, although predictions for summer rainfall vary from slight increases to decreases, and precipitation projections are much less certain than those for temperature (Garfin et al. 2013; IPCC 2013; Swain and Hayhoe 2014). While there remains debate over validity of projections of global drought intensity and frequency (Sheffield et al. 2012; Zhou and Hong 2013), most models project increased regional climatic variability, most importantly including increased drought severity in the North American West and Southwest (Ault et al. 2014; Cayan et al. 2010; Cook et al. 2014; Gershunov et al. 2013; Seager et al. 2007, 2014; Trenberth et al. 2014). These projections predict that *G. morafkai* will face additional episodes of elevated mortality in the coming decades that will exceed those associated with population reductions seen during the past 2.5 decades. Whether possible density dependent resilience following abundance reductions (Chapter 4) like those reported here will forestall local extinctions is unpredictable from the results reported here.

No observed population of *G. morafkai* outside of urban or semi-urban environments is known or suspected to have become extinct in recent times (USFWS 2010). However, most observed populations are in relatively high-quality habitat, and there are no published data and little anecdotal information from areas within the known distribution where climatic stress is most severe and where population extinctions are likely to first occur (or have already occurred): lower Gila River and Colorado River valley regions in southwestern-most Arizona and the Pinacate region of northwestern Sonora. Although mortality episodes have been observed in all occupied biotic communities except for tropical deciduous forest (where a genetically divergent population exists; Edwards et al., *submitted*), the most pronounced mortality episodes and abundance reductions are located peripherally to a population core for genetically Sonoran *G. morafkai*, often in low elevation, arid or very hot environments (Chapters 2-4).

G. morafkai lives across a broad elevational range (0-1100 m, with rare occurrences of populations up to 1525 m) and over 10 degrees of latitude, corresponding to an ≈ 8 C range of mean annual temperature (≈ 16.9 to 24.8 C, to ≈ 26.1 C for the Sinaloan genetic group), although most are 19-24 C. This range exceeds most projections for air temperature increase in the Southwest by the year 2080 (2.6 – 4.4 C under different scenarios; Garfin et al 2013), suggesting that thermal stress, alone, would not eliminate the species from its current range under climate change by 2080. However, most populations are within

a ≈ 5 C envelope of mean annual temperatures; and, further, direct effects of rising temperatures coupled with indirect effects of temperature on drought severity and frequency pose a probable threat to the species.

The recurrent and sometimes severe drought conditions associated with the tortoise declines reported here are related to long-term (multi-decadal) climate flux (Dai 2013), as well as shorter-term fluxes such as ENSO effects on winter precipitation (Dominguez et al. 2009), which are driven by sea-surface temperatures (Seager and Hoerling 2014). Assuming that these recurrent climatic patterns are in a drought-ameliorated phase in the near decades, tortoise populations may experience some recovery, but a subsequent return of arid-phase climate conditions under a hotter temperature regime (e.g., Breshears et al. 2005), even without any decrease in seasonal precipitation or climatic variability (Fu and Feng 2014; Scheff and Frierson 2014; Weiss et al. 2012), will add to nutritional, water-balance, and other stresses affecting homeostasis in desert tortoises. If the multi-decadal wet-dry climatic periodicity holds at about 40-50 years, *G. morafkai* is likely to face a drought challenge at or near mid-century more stringent than the one described herein.

What is particularly troubling about the existing record is the absence of favorable population responses along the less arid and hot northern and northeastern range margins, where climatic stress can be predicted to be less severe for this tortoise, and where shifts upward in elevation in response to climatic heating and drying would *prima facie* seem most plausible. Instead, those populations that have appeared to remain relatively stable, and largest, tend to be in the core of Arizona Upland Sonoran Desertscrub (Chapters 2-4). Further, buffelgrass spread, fire in both buffel and Interior Chaparral, and hard freezes may obstruct up-migration population responses.

Results presented and discussed herein demonstrate that demographic study focused on abundance and adult mortality are critical to the conservation biology of *G. morafkai*, not only in core regions where population collapse is not yet observed, but in unstudied regions where tortoise abundance is low and climatic stress most extreme.

Results of this study demonstrate that mortality, which is primarily detected as carcasses of larger, older tortoises, has driven the larger observed population declines. Nonetheless, our extreme ignorance should be remedied about populational and physiological ecology of smaller, younger tortoises – which are very likely the most climate-sensitive population members (Hillard, 1996; Esque et al. 2014; Nagy et al. 1997; Wilson et al. 2001), and are the key signal for population recovery and maintenance. Although the statistical analysis presented in this report failed to demonstrate an effect of recruitment on population change, inspection of the sequence of body size histograms for all of the intensive census plots (Appendix 1 and sources cited therein) clearly shows that recruitment into the adult size class was occurring for most study areas during 1987-2010. Detailed analysis of these data, which in aggregate over the 17 or more study areas are quite substantial, is especially warranted by the need to elucidate demographic processes in juvenile tortoises.

Physiological ecology of desert tortoises has been studied almost exclusively in *G. agassizii* in Mojave Desert, but findings should apply in a general for drought effects in *G. morafkai*. Although widespread,

catastrophic declines in *G. agassizii* over more than three decades have been attributed to numerous proximate causes, most importantly from the standpoint of potential intractability to conservation efforts, drought-caused physiological stress may be an overriding ultimate driver of mortality and population decline. Under water stress, tortoises in Mojave Desert have high, rising bladder and blood osmolality, declining total body water, greatly reduced metabolic and water flux rates, and elevated blood nitrogen that may reflect starvation (Peterson 1994, 1996a&b, Nagy and Medica 1986; Henan et al. 1998), among which body water and osmolality were in worse conditions at a site where many tortoises were dying with drought-related physiological stress (Peterson 1994, 1996b). However, whether desiccation or starvation, or both individually or interacting, kill desert tortoises during drought is not clear. In Mojave Desert, physiologically caused death was associated with two-year periods of drought; this might apply to *G. morafkai* in Sonoran Desert, despite the higher annual ($\approx 130\text{-}330$ mm vs. $90\text{-}190$ mm) and bi-seasonal (winter-spring and summer vs. winter-spring) rainfall regime in Sonoran Desert versus Mojave Desert tortoise habitat (Turner 1982; Turner and Brown 1982). However, *G. morafkai* does not necessarily have the same absolute drought tolerance as *G. agassizii*.

A suggestive finding in the present study is the appearance of heavy mortality significantly in advance of drought nadirs (Table 5.1; Fig. 5.14). A methodological caveat here is that decomposition rates of tortoise carcasses under varying precipitation have not been measured in the Sonoran Desert. However, for some of the mass mortality episodes, large numbers of carcasses were definitively found and assigned to year-of-death prior to drought nadir year. This suggests that drought related stress, whether from nutritional shortfall or failing water and solute balance, may develop rapidly in *G. morafkai* early in drought conditions that follow years of strong rainfall. Although in Sonoran Desert annual precipitation extremes vary by $\approx 4\text{-}6$ -fold over 30 year periods, production of ephemeral plants as tortoise food in the warm deserts may often vary by more than 2 orders of magnitude in successive years (Duda et al. 2009; Medica et al. 1982), and such low productivity is not restricted to years or seasons of severe drought. Physiological research is thus much needed in the conservation biology of *G. morafkai*, along with behavioral response to drought, time and cause of death observations, more refined and detailed climatic correlations than were attempted herein, and more refined calculations of drought-related demographics with existing and continuing census data.

A major obstacle to clarifying these processes is the absence of growth ring data that, with repeat digital photographs, could be utilized to demonstrate age structure, juvenile survivorship profiles, and age-at-maturity, none of which are currently known for *G. morafkai* to much closer than an order of magnitude. Use of age structure based on growth rings, even if not exact to 1-2 years of age, will facilitated population estimation and demographic modeling.

Although the record of episodic mortality in *G. morafkai* presented in Table 5.1 spans more than half of the period of rapidly rising regional temperatures that began in the 1960's, these are neither the first nor entirely unique drought instances in recent, post-Wisconsin millennia (Cook et al. 2004, 2009; Garfin et al. 2013; Routson et al. 2011; Seager et al. 2009; Stahle et al. 2000; Woodhouse et al. 2010). Bury and Corn (1995) argued that contrary to conventional wisdom, tortoise abundances in Mojave Desert may have been far lower 6-15+ decades ago than they were 3-5 decades ago prior to recently observed population collapses there. We know little about historic and pre-historic tortoise abundance and

climatic relations, but population trend results from recent decades in the Sonoran and Mojave deserts, coupled with environmental correlates and climate projections, should alone be cause for conservation concern.

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Appendix 1. Data used for demographic and abundance analyses, modified and updated from Averill-Murray et al. (2002). Abundance has been scaled to the predominant plot size of 2.56 km² (1 square mile), but not corrected for boundary effects on population estimates.

Plot Name	YEAR	No. of individuals: F-M-Juv-Dead	% JUV unsexed	% DEAD in YR sample	Effort (person-d)	POP_EST	other abundance estimates	Sources
Alamo Hill, Hualapai Mts	1980	12 / 10 / 7 / 8	24.1%	21.6%	22		≈100	Schneider 1981
Arrastra, Poachie Mts	1987	9 / 6 / 3 / 16	16.7%	47.1%	>60	20.0		Wirt 1988
Arrastra, Poachie Mts	1997	8 / 5 / 1 / 2	7.1%	12.5%	35		24.0	Woodman et al. 1998
Arrastra, Poachie Mts	2002	4 / 3 / 0 / 2	0.0%	22.2%	36	7.0		Woodman et al. 2003
Arrastra, Poachie Mts	2006	5 / 3 / 1 / 0	11.1%	0.0%	20	7.8		Woodman et al. 2007
Bonanza Wash, Grayback Mts	1992	6 / 8 / 3 / 13	17.6%	43.3%	62	28.0		Woodman et al. 1993
Bonanza Wash, Grayback Mts	1997	4 / 6 / 3 / 2	23.1%	13.3%	35		27.0	Woodman et al. 1998
Bonanza Wash, Grayback Mts	2002	7 / 6 / 2 / 2	13.3%	11.8%	35	17.0		Woodman et al. 2003
Bonanza Wash, Grayback Mts	2006	5 / 7 / 4 / 0	25.0%	0.0%	19	17.2		Woodman et al. 2007
Buck Mts	2002	13 / 8 / 2 / 6	8.7%	20.7%	33	21.0		Woodman et al. 2003
Buck Mts	2005	9 / 6 / 1 / 9	6.3%	36.0%	38	17.0		Woodman et al. 2006
Buck Mts	2010	4 / 7 / 1 / 1	8.3%	7.7%	35	12.8		EcoPlan, Inc. 2011
E Bajada, Black Mts	1990	12 / 21 / 12 / 5	26.7%	10.0%	86	65.0		SWCA, Inc. 1990a
E Bajada, Black Mts	1993	14 / 29 / 3 / 10	6.5%	17.9%	60		67.0	Woodman et al. 1994
E Bajada, Black Mts	1997	23 / 20 / 2 / 6	4.4%	11.8%	60		61.0	Woodman et al. 1998
E Bajada, Black Mts	2002	3 / 5 / 1 / 47	11.1%	83.9%	60	9.0		Woodman et al. 2003
E Bajada, Black Mts	2007	7 / 8 / 1 / 0	6.3%	0.0%	11	17.0		Woodman et al. 2008
Eagletail Mts	1987	22 / 12 / 8 / 8	19.0%	16.0%	52	32.3		Shields and Woodman 1987
Eagletail Mts	1990	21 / 8 / 3 / 1	9.4%	3.0%	61	30.0		Shields et al. 1990
Eagletail Mts	1991	16 / 9 / 7 / 5	21.9%	13.5%	36	29.0		Hart et al. 1992
Eagletail Mts	1992	12 / 10 / 5 / 1	18.5%	3.6%	35	30.0		Woodman et al. 1993
Eagletail Mts	1993	13 / 10 / 14 / 3	37.8%	7.5%	35	30.0		Woodman et al. 1994
Eagletail Mts	1994	17 / 11 / 19 / 9	40.4%	16.1%	35		30.0	Woodman et al. 1995
Eagletail Mts	1998	17 / 14 / 8 / 5	20.5%	11.4%	35		30.0	Woodman et al. 1999
Eagletail Mts	2003	18 / 8 / 4 / 11	13.3%	26.8%	40	27.0		Woodman et al. 2004
Eagletail Mts	2007	12 / 6 / 3 / 1	14.3%	4.5%	29	18.6		Woodman et al. 2008
Granite Hills, Picacho Mts	1990	16 / 16 / 16 / 8	33.3%	14.3%	66	63.0		Shields et al. 1990
Granite Hills, Picacho Mts	1991	30 / 19 / 21 / 4	30.0%	5.4%	60	60.0		Hart et al. 1992
Granite Hills, Picacho Mts	1992	23 / 22 / 30 / 2	40.0%	2.6%	60	69.0		Woodman et al. 1993
Granite Hills, Picacho Mts	1993	31 / 24 / 40 / 2	42.1%	2.1%	60	69.0		Woodman et al. 1994
Granite Hills, Picacho Mts	1994	31 / 29 / 49 / 3	45.0%	2.7%	60	69.0		Woodman et al. 1995
Granite Hills, Picacho Mts	1998	20 / 16 / 20 / 13	35.7%	18.8%	60		60.0	Woodman et al. 1999
Granite Hills, Picacho Mts	2003	35 / 14 / 15 / 8	23.4%	11.1%	60	69.0		Woodman et al. 2004
Granite Hills, Picacho Mts	2007	24 / 14 / 7 / 5	15.6%	10.0%	36	50.0		Woodman et al. 2008

Table Continued

Plot Name	YEAR	F-M-Juv-Dead	% JUV (unsexed)	% DEAD in YR sample	Effort (person- d)	POP_EST	other abundance estimates	Sources
Harcuvar Mts	1988	22 / 32 / 4 / 8	6.9%	12.1%	68	63.3		Trachy and Dickenson 1993
Harcuvar Mts	1993	15 / 29 / 2 / 5	4.3%	9.8%	64		72.0	Woodman et al. 1994
Harcuvar Mts	1997	23 / 27 / 4 / 6	7.4%	10.0%	60		77.0	Woodman et al. 1998
Harcuvar Mts	2002	18 / 24 / 4 / 6	8.7%	11.5%	60	51.9		Woodman et al. 2003
Harcuvar Mts	2006	19 / 27 / 10 / 15	17.9%	21.1%	45	50.8		Woodman et al. 2007
Harquahala Mts	1988	9 / 8 / 4 / 4	19.0%	16.0%	67	12.0		Holm 1989
Harquahala Mts	1994	10 / 7 / 2 / 0	10.5%	0.0%	60.5		15.0	Woodman et al. 1995
Harquahala Mts	2001	2 / 5 / 1 / 8	12.5%	50.0%	35	9.5		Woodman et al. 2002
Harquahala Mts	2004	1 / 6 / 0 / 1	0.0%	12.5%	28	8.0		Woodman et al. 2005
Hualapai Foothills	1991	13 / 19 / 5 / 8	13.5%	17.8%	47	46.4		Hart et al. 1992
Hualapai Foothills	1996	13 / 21 / 2 / 6	5.6%	14.3%	45	37.1		Woodman et al. 1997
Hualapai Foothills	2001	10 / 5 / 0 / 11	0.0%	42.3%	45	16.0		Woodman et al. 2002
Hualapai Foothills	2005	5 / 6 / 6 / 11	35.3%	39.3%	32	11.9		Woodman et al. 2006
Little Shipp Wash	1990	42 / 26 / 16 / 9	19.0%	9.7%	61	85.0		Shields et al. 1990
Little Shipp Wash	1991	37 / 30 / 15 / 2	18.3%	2.4%	60	107.0		Hart et al. 1992
Little Shipp Wash	1992	42 / 34 / 12 / 2	13.6%	2.2%	60	107.0		Woodman et al. 1993
Little Shipp Wash	1993	47 / 36 / 20 / 9	19.4%	8.0%	60	97.0		Woodman et al. 1994
Little Shipp Wash	1994	34 / 27 / 16 / 3	20.8%	3.8%	60		97.0	Woodman et al. 1995
Little Shipp Wash	1998	30 / 18 / 10 / 9	17.2%	13.4%	60		98.0	Woodman et al. 1999
Little Shipp Wash	2003	35 / 23 / 14 / 6	19.4%	7.7%	60	65.1		Woodman et al. 2004
Little Shipp Wash	2007	29 / 24 / 14 / 3	20.9%	4.3%	45	62.2		Woodman et al. 2008
Maricopa Mts	1987	24 / 33 / 1 / 65	1.7%	52.8%	58	172.5		Wirt 1987, 1995; Wirt and Holm 1997a
Maricopa Mts	1990	6 / 7 / 4 / 54	23.5%	76.1%	60			Wirt 1987, 1995; Wirt and Holm 1997a
Maricopa Mts	2000	8 / 9 / 3 / 4	15.0%	16.7%	60	19.6		Woodman et al. 2001
Maricopa Mts	2005	6 / 13 / 2 / 2	9.5%	8.7%	47	20.1		Woodman et al. 2006
Mazatzal Mts	1992	19 / 27 / 5 / 8	9.8%	13.6%	56	150.0		Murray 1993; Murray & Schwalbe 1997
Mazatzal Mts	1995	24 / 25 / 17 / 3	25.8%	4.3%	56	114.0		Murray and Schwalbe 1997
Mazatzal Mts	2001	20 / 20 / 6 / 13	13.0%	22.0%	60	125.0		Woodman et al. 2002
New Water Mts	1988	8 / 7 / 1 / 2	6.3%	11.1%	46	15.0		Shields and Woodman 1988
New Water Mts	1999	9 / 8 / 5 / 3	22.7%	12.0%	35	32.0		Woodman et al. 2000
New Water Mts	2003	14 / 9 / 3 / 2	11.5%	7.1%	25	26.6		Woodman et al. 2004
New Water Mts	2007	14 / 9 / 3 / 3	11.5%	10.3%	18	32.3		Woodman et al. 2008
Organ Pipe NM, Ajo Mtn Dr	1996	11 / 12 / 6 / 8	20.7%	21.6%	45		75.0	Wirt et al. 1999
Organ Pipe NM, Quitobaquito Hills	1997	16 / 6 / 3 / 1	12.0%	3.8%	45		34.0	Wirt et al. 1999
Organ Pipe NM, Twin Peaks	1996	9 / 6 / 0 / 0	0.0%	0.0%	45		28.0	Wirt et al. 1999
Ragged Top, Silverbell Mts	1980	na			27		<75	Schneider 1981

Table Continued

Plot Name	YEAR	F-M-Juv-Dead	% JUV (unsexed)	% DEAD in YR sample	Effort (person- d)	POP_EST	other abundance estimates	Sources
Saguaro NP, Rincon Mts, Burn	1996	13 / 12 / 9 / 6	26.5%	15.0%	45		116.0	Wirt and Robichaux 2001
Saguaro NP, Rincon Mts, Javelina	1996	18 / 29 / 15 / 2	24.2%	3.1%	45		148.5	Wirt and Robichaux 2001
Saguaro NP, Rincon Mts, Javelina	1997	29 / 29 / 18 / NA	23.7%		46		160.0	Wirt and Robichaux 2001
Saguaro NP, Tucson Mts,	1996	25 / 24 / 22 / 12	31.0%	14.5%	45		130.6	Wirt and Robichaux 2001
Saguaro NP, Tucson Mts,	1997	35 / 23 / 26 / NA	31.0%		46		129.3	Wirt and Robichaux 2001
San Pedro Valley	1991	18 / 16 / 9 / 11	20.9%	20.4%	60			Hart et al. 1992
San Pedro Valley	1995	36 / 48 / 6 / 9	6.7%	9.1%	60	125.0		Woodman et al. 1996
San Pedro Valley	2001	5 / 16 / 6 / 46	22.2%	63.0%	60	39.0		Woodman et al. 2002
San Pedro Valley	2004	7 / 21 / 6 / 5	17.6%	12.8%	60	30.6		Woodman et al. 2005
San Pedro Valley	2008	7 / 15 / 5 / 1	18.5%	3.6%	29	45.0		Woodman et al. 2009
Sand Tank Mts *	1992	19 / 15 / 0 / 31	0.0%	47.7%				GeoMarine 1994, Wirt & Holm 1997b
Sand Tank Mts *	1994	2 / 5 / 6 / 32	46.2%	71.1%				Dames and Moore 1994
Tortilla Mts	1992	29 / 20 / 3 / 12	5.8%	18.8%	60	85.1		Woodman et al. 1993
Tortilla Mts	1996	34 / 26 / 12 / 9	16.7%	11.1%	60		97.0	Woodman et al. 1997
Tortilla Mts	2001	26 / 22 / 4 / 1	7.7%	1.9%	60	69.0		Woodman et al. 2002
Tortilla Mts	2006	38 / 29 / 10 / 6	13.0%	7.2%	44	100.0		Woodman et al. 2007
W Silverbell Mts	1991	39 / 20 / 5 / 11	7.8%	14.7%	60	121.9		Hart et al. 1992
W Silverbell Mts	1995	40 / 35 / 16 / 8	17.6%	8.1%	60		134.0	Woodman et al. 1996
W Silverbell Mts	2000	62 / 39 / 10 / 13	9.0%	10.5%	60	147.0		Woodman et al. 2001
W Silverbell Mts	2004	24 / 15 / 39 / 14	50.0%	15.2%	62	140.0		Woodman et al. 2005
W Silverbell Mts	2008	40 / 29 / 8 / 7	10.4%	8.3%	27	96.5		Woodman et al. 2009
Wickenburg Mts	1991	5 / 10 / 0 / 2	0.0%	11.8%	60			Hart et al. 1992
Wickenburg Mts	2000	6 / 9 / 3 / 2	16.7%	10.0%	35	19.0		Woodman et al. 2001
Wickenburg Mts	2004	8 / 10 / 8 / 0	30.8%	0.0%	36	18.5		Woodman et al. 2005
Wickenburg Mts	2008	9 / 9 / 4 / 1	18.2%	4.3%	20	14.2		Woodman et al. 2009

** Sand Tank Mountains data are from different sets of plots in the two years.

Appendix 2. Plot census schedule for study of desert tortoises in the Sonoran Desert of Arizona.

SITE	1980	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	Σ years	
<i>Alamo Hill</i>	x																									1	
<i>Arrastra Mts</i>		X										X					X				X						4
<i>Black Butte</i>	x																										1
<i>Bonanza Wash</i>							X					X					X				X						4
<i>Buck Mts</i>																	X			X						X	3
<i>E Bajada</i>					X			X				X					X						X				5
<i>Eagletail Mts</i>		X			X	X	X	X	X				X					X					X				9
<i>Granite Hills</i>					X	X	X	X	X				X					X					X				8
<i>Harcuvar Mts</i>	x		X					X				X					X				X						6
<i>Harquahala Mts</i>			X						X							X			X								4
<i>Hualapai Foothills</i>						X					X					X					X						4
<i>Javelina Picnic</i>											x	x															2
<i>Little Shipp Wash</i>	x				X	X	X	X	X				X					X					X				9
<i>Maricopa Mts</i>		X			X										X					X							4
<i>Mazatzal Mts</i>							X			X						X											3
<i>Mothers Day Burn</i>											x																1
<i>New Water Mts</i>			X											X				X					X				4
<i>Panther Peak</i>											x	x															2
<i>Ragged Top</i>	x																										1
<i>San Pedro Valley</i>						X				X						X			X					X			5
<i>Sand Tank Mts</i>							x		x																		2
<i>Tortilla Mts</i>							X				X					X						X					4
<i>W Silverbell Mts</i>						X				X					X				X					X			5
<i>Wickenburg Mts</i>						X									X				X					X			4
Total plots	5	3	3	0	5	7	7	5	5	3	5	6	3	1	3	5	5	4	4	3	4	5	3	0	1	95	
Re-census plots	0	3	3	0	5	7	6	5	4	3	2	4	3	1	3	5	5	4	4	3	4	5	3	0	1	83	

Chapter 6 Preliminary Report on Operative Temperatures for Desert Tortoises in Tropical Deciduous Forest and Desertscrub Mexico

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ABSTRACT

We used operative temperatures models shaped like tortoises to portray the operative thermal environment of desert tortoises (*Gopherus morafkai*) in three environments in Mexico during October 2012 – August 2013. Cooler, shadier thermal characteristics of tropical deciduous forest (TDF) in southern Sonora permit tortoise activity for $\approx 3X$ longer per day in forest than in coastal desertscrub, based on 12 days of comparative data in early October, and the effect is likely greater at hotter times of year. Induced buffelgrass (*Pennisetum ciliare*) pasture, which is the term used for created pasture in wildlands in Mexico) within the TDF biome was intermediate between these extremes, though more similar to desertscrub. Hours of thermally-imposed restriction of tortoise activity in pasture during March-August (6-10 hr/day) were far greater than in TDF (0.4-2.5 hr/day), although there was little effect in October, when we found tortoises in the pastures, which had warmer, more favorable temperatures for tortoise activity. “Sinaloan” tortoises in TDF are genetically divergent from Sonoran *G. morafkai* (Edwards et al., submitted), and may experience selection for a unique thermal physiology, but the Sinaloan genotype also occurs in very hot low-elevation thornscrub, which may constrain adaptation to the T_e characteristics of TDF. The altered thermal regime of induced pastures poses a threat to desert tortoises in TDF and very likely in thornscrub, but conservation efforts permitting successional processes would likely allow both these biotic communities to restore a more favorable thermal environment for terrestrial turtles.

6.1 INTRODUCTION

Gopherus morafkai (Morafka’s, or Sonoran Desert, tortoise) is currently being evaluated for listing as threatened under the U.S. Endangered Species Act (USFWS 2010), which would focus efforts to protect and recover the species. Little information has previously been available for the 40% of *G. morafkai*’s geographic range that is in Mexico. Elsewhere in this report we describe climate-associated mortality episodes in Mexico during at least 1998-2011 (Chapters 2 and 3) that are similar to those observed in this species in Arizona (Chapters 4 and 5) and are inferred to have resulted in population declines in at least some of the areas with elevated mortality (Chapter 2). In Chapter 1, in which we present

evaluations of the conservation status and threats to this tortoise in Mexico, ongoing and projected anthropogenic climate warming and expected increases in drought frequency and severity are identified as the largest threat to the species in Mexico and throughout its range.

Drought has been cited as a driver of some or many episodes of high mortality and population decline in the federally threatened *G. agassizii* (Agassiz's, or Mojave Desert tortoise; Berry et al. 2002; Field et al. 2007; Germano and Joyner 1989; Karl 2004; Longshore et al. 2003; Lovich et al. 2014; Peterson 1994, 1996a&b), although in some cases drought acts indirectly through elevated predation (Berry et al. 2002; Esque et al. 2010) or may be proximately (Tracy et al. 2004) or ultimately caused by the disease mycoplasmosis (Berry 1997). Recent climate-niche modeling (Barrows 2011) and long-term population study (Lovich et al. 2014) explicitly demonstrate a climate threat in *G. agassizii*. However, an analysis of prospective climate change impacts on animals in the U.S. Southwest (van Riper et al. 2014) concluded that *G. morafkai* would be little affected, whereas Sinervo (2014) predicted an overwhelming effect over the next 65-85 years.

Average annual temperature in the arid Southwest of North America has already increased by about 1.5 C during the last five decades and is projected to further increase by 1.5 – 8.5 C, depending on anthropogenic global warming gas production and climate model structure, during the current century (Garfin et al. 2013). Population declines and episodic high mortality observed in *G. morafkai* in Arizona and Sonora during 1989-2011 were associated with drought and high temperature phenomena (Chapters 2 and 5) that are extremely likely to recur in exacerbated form over the next several decades and could drive the species toward extinction within large portions of its current range.

Although drought was the best predictor of mortality rates and abundance declines in *G. morafkai* (Zylstra et al. 2012; Chapter 5), high temperature anomalies were also correlated with mortality (Chapters 2 and 5). In the southern region of Sinaloa thornscrub in Sonora, Mexico, precipitation is higher than in most regions where elevated mortality episodes have been observed in *G. morafkai* in Arizona and Sonora, which might be expected to mitigate drought effects (Chapter 2). However, this is also the hottest region occupied by *G. morafkai*; thus direct effects of temperature on survivorship and reproduction may be involved there. In contrast, we found no evidence of elevated mortality in desert tortoises in the tropical deciduous forest (TDF) of southern Sonora and northern Sinaloa, a biome with a combination of lower temperatures and higher precipitation than elsewhere in the species' range.

Other tortoises (Barrows 2011; Loehr et al. 2009; Sinervo 2014) and reptiles (Huey et al 2010; Sinervo et al. 2010), and many other long-lived organisms (Allen et al. 2010; Breshears et al. 2009) are highly sensitive to effects of anthropogenic global warming, and threats are often driven by climate change-related drought. Indeed, climate change impacts on a multitude of species are driven by interactions with other stressors. In our evaluation, the second greatest threat facing *G. morafkai* in Mexico (Chapter 1) is the planting of exotic buffelgrass (*Pennisetum ciliare*) over millions of hectares of induced pasture in northwestern Mexico and its further self-proliferation into core tortoise habitat. In addition to enhanced fire regimes (Esque et al. 2002, 2003) and effects on desert tortoise food base (Gray 2012), conversion of native vegetation to induced pasture likely changes the operative thermal environment (T_e) of desert tortoises.

Physiological ecology (Bakken 1992; Bakken and Gates 1975; Porter and Tracy 1982; Porter et al. 1973;) is key to understanding and projecting climatic effects on desert tortoises (Bulova 1994, 2002; Duda et al. 1999; Henan et al. 1998; McGinnis and Voigt 1971; Nagy and Medica 1986; Peterson et al. 1994, 1996a&b; Ruby et al. 1994; Voigt 1975; Wilson et al. 2001; Zimmerman et al. 1994) and other reptiles (e.g., Adolph et al 1993; Deutch et al. 2008; Dunham 1993; Dunham et al. 1989; Grant 1990; Grant and Porter 1992; Huey et al 2010; Kearny 2013; Sinervo et al. 2010; Tracy et al. 2006). Key to this is measurement of operative environments, the biophysical conditions experienced by organisms in their habitats (Bakken 1992; Grant and Porter 1992; Dunham et al. 1989; Paranjpe et al. 2012). In this chapter we present the first data on operative temperatures for desert tortoises in tropical deciduous forest habitats, comparing primary forest with induced pasture and low elevation Sonoran Desertscrub (Figs. 1 and 2).



Figure 6.1. T_e study areas in Central Gulf Coast Sonoran Desertscrub (left) and Tropical Deciduous Forest (right).

6.2 METHODS

We constructed model tortoises made of copper and covered with paint to match the absorbance of solar radiation of tortoises (Fig. 6.2). Temperature data loggers (Onset HOBOTM) were anchored inside the models, which were sealed with silicon glue and placed in tortoise habitat in a range of exposure directions, microenvironments, and shade conditions (Table 6.1). We set 4 models in TDF and 2 in a buffelgrass pasture within TDF near Alamos, and 4 in Central Gulf Coast Sonoran Desertscrub in early October 2012 and collected simultaneous T_e readings for 12 days. We then moved all models to the Alamos region, where we recorded T_e from October 2012 through August 2013 with 4 models in induced buffelgrass pasture, and 10 models in primary TDF (4 at Rancho El Palomar with lowlands as induced buffelgrass pastures and 6 in montane TDF at Rancho La Sierrita).

Data logger batteries were replaced and additional models were installed in 2013 and downloaded in October 2014, and tortoise body temperatures were recorded in October 2014, but these results are not included here.



Figure 6.2. Tortoise T_e models and microhabitat in Tropical Deciduous Forest (above) and induced buffelgrass pasture (below). The model in full sun (above, left) is encircled by stakes to discourage cattle trampling. The model in buffel (lower left) was the most exposed to insolation of any in that environment type.

Final download dates are shown in Table 6.1. Data were inspected graphically and trimmed in HOBOWare™ data logger software and Microsoft Excel™ to eliminate bad readings, start-end sequences, and partial days. Sunrise and sunset data for Hermosillo, Sonora were used to set daily start and end brackets for computation of thermal parameters for tortoise activity based on an assumption, which remains untested, that tortoise activity occurs primarily during daylight hours. We used Zimmerman et al.'s (1994) thermal activity range (26-35 C) for *G. agassizii* for preferred activity temperature range (T_p), although this has not been reported for either Sonoran or Sinaloan *G. morafkai* genotypes (see Edwards et al. 2012, and *submitted*). Using Sinervo et al.'s (2010) definition, we computed potential activity times (hours of activity, h_a = time T_e is within T_p) and time when *G. morafkai* would be thermally constrained by high T_e from surface activity (hours of restriction of activity, h_r). We used critical thermal maximum estimates (summarized by Ernst and Lovich 2009) for graphical purposes.

One of the T_e models in induced pasture was placed flush in the base of a dense clump of buffelgrass, which would usually be a shelter or resting position for tortoises, as food would likely be scarce there. We therefore present h_a and h_r with and without data from this T_e model. Data are presented here as means \pm 1 standard error.

Table 6.1. Operative temperature model locations, run durations, and environmental parameters, Mexico, October 2012-August 2013.

Location	Macrohabitat	Microhabitat	Start Date	End Date	UTM (WGS 1984)	Elev. (m)	ID
Alamos, El Palomar	Buffel vale	shade, buffel	19-Oct-12	21-Aug-13	12 R 702981 2993800	424	REP-bfl-02
Alamos, El Palomar	Buffel vale	shade, Acacia shrub	19-Oct-12	21-Aug-13	12 R 702982 2993794	423	REP-bfl-03
Alamos, El Palomar	Buffel vale	shade, buffelgrass base	2-Oct-12	21-Aug-13	12 R 703262 2993715	427	REP-bfl-04
Alamos, El Palomar	Buffel vale	sun, filtered, grass clump margin	2-Oct-12	21-Aug-13	12 R 703261 2993713	434	REP-bfl-01
Alamos, El Palomar	TDF hills	sun, filtered	19-Oct-12	10-Aug-13	12 R 702984 2993920	453	REP-TDF-01
Alamos, El Palomar	TDF hills	shade, filtered	19-Oct-12	10-Aug-13	12 R 702984 2993921	452	REP-TDF-02
Alamos, El Palomar	TDF hills	shade, filtered	19-Oct-12	10-Aug-13	12 R 702982 2993926	453	REP-TDF-03
Alamos, El Palomar	TDF hills	shade, filtered, forb	19-Oct-12	10-Aug-13	12 R 702982 2993928	460	REP-TDF-04
Alamos, La Sierrita	TDF mountains	shade, rock, NE exposure	18-Oct-12	10-Aug-13	12 R 703942 2984965	550	RLS-TDF-05
Alamos, La Sierrita	TDF mountains	shade, filtered, NE exposure	18-Oct-12	10-Aug-13	12 R 703942 2984971	547	RLS-TDF-06
Alamos, La Sierrita	TDF mountains	shade, rock-filtered, N exposure	1-Oct-12	10-Aug-13	12 R 703942 2984903	550	RLS-TDF-04
Alamos, La Sierrita	TDF mountains	sun, partial, E exposure	1-Oct-12	10-Aug-13	12 R 703942 2984899	548	RLS-TDF-01
Alamos, La Sierrita	TDF mountains	sun, filtered, S exposure	1-Oct-12	10-Aug-13	12 R 703938 2984899	549	RLS-TDF-02
Alamos, La Sierrita	TDF mountains	shade, W exposure	1-Oct-12	10-Aug-13	12 R 703934 2984905	553	RLS-TDF-03
Punta Chueca	Desert hill	sun	4-Oct-12	16-Oct-12	12 R 391967 3206589	71	DS-01
Punta Chueca	Desert hill	shade, filtered, shrub	4-Oct-12	16-Oct-12	12 R 391967 3206589	74	DS-02
Punta Chueca	Desert hill	shade, filtered, tree, N side	4-Oct-12	16-Oct-12	12 R 391972 3206593	75	DS-03
Punta Chueca	Desert hill	shade, filtered, tree, S side	4-Oct-12	16-Oct-12	12 R 391973 3206588	76	DS-04

6.3 RESULTS

6.3.1 Comparison of Desertscrub, TDF, and Buffel Pasture

Comparative data for three habitats measured simultaneously on sunny days in early October 2012 are displayed in Fig. 6.3. In coastal desertscrub, all of the T_e models rapidly warmed in morning and cooled in early evening through the range of T_p , and all reached lethal temperatures during midday for several hours. There was a similar pattern in the buffel grass pasture in the TDF region of Alamos, except that the model nestled into the base of a dense bunch of buffelgrass warmed more gradually and did not reach lethal temperatures. In TDF, all models warmed into the T_p range in the morning and remained in it until the end of the afternoon.

Thermal activity windows (h_a) and hours of restriction of activity by high temperature (h_r) for the same three habitats in early October are shown in Fig. 6.4A. In TDF, the T_e during daylight hours was suitable for activity for 6.7 hr/d and almost never exceeded T_p ($h_r \approx 0$). T_e in buffel pasture within TDF were suitable for activity for 4.5 hr/d, while $h_r = 4.6$ hr/day. In coastal desertscrub, h_a was 2.2 hr/day while $h_r = 7.9$ hr/day. Thus, buffel pasture was intermediate between TDF with high thermal suitability for desert tortoises and desertscrub with low suitability. However, excluding the shaded base of the buffelgrass clumps, thermal quality in the buffelgrass pasture was almost as low as that of desertscrub (Fig. 6.4B), although all means were significantly different ($P < 0.01$) among habitats.

6.3.2 Comparison of Primary TDF and Buffel Pasture near TDF

An example of a monthly summary of T_e for all of the tortoise models in Alamos is shown in Fig. 6.5. In buffelgrass pasture in August 2013, all model temperatures rose through the T_p range in about 2 hr during the morning, except the model nestled into the buffelgrass clump base. Model temperatures rapidly progressed into and well over lethal limits measured for *G. agassizii*, before descending through the T_p range for about 2.5 hr during the late afternoon to early evening. Even in the grass clump base, model temperatures approach lower lethal limits, on average, during mid-afternoon. In primary TDF, model temperatures rose slowly to midday plateaux or peaks within the T_p range before descending through the T_p range for about 2.5 hr during late afternoon or at night.

Data for h_r and h_a through the year are summarized in Fig. 6.6. Hours of high-temperature thermal restriction (h_r) were much higher in buffel pasture than in TDF throughout the entire year except December, when there was no restriction in either habitat type. Time available for activity (h_a) based on T_e was higher in TDF than in buffel pasture at least March – August, but this was reversed during October and November.

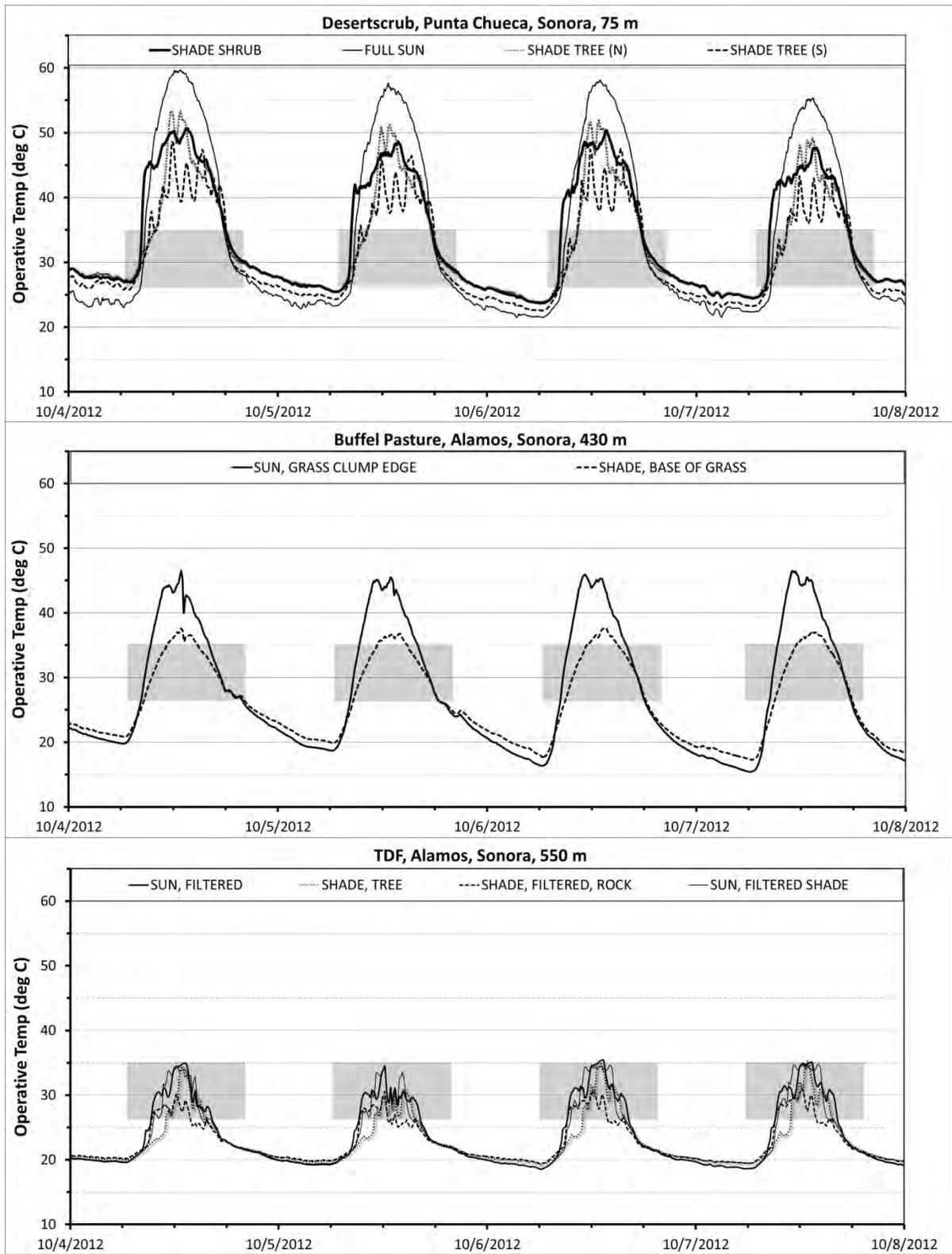


Figure 6.3. T_e for *Gopherus morafkai* in three environments in Mexico measured simultaneously on warm sunny days. Gray bars portray T_p for desert tortoises, which has been reported only for *G. agassizii* in Mojave Desert.

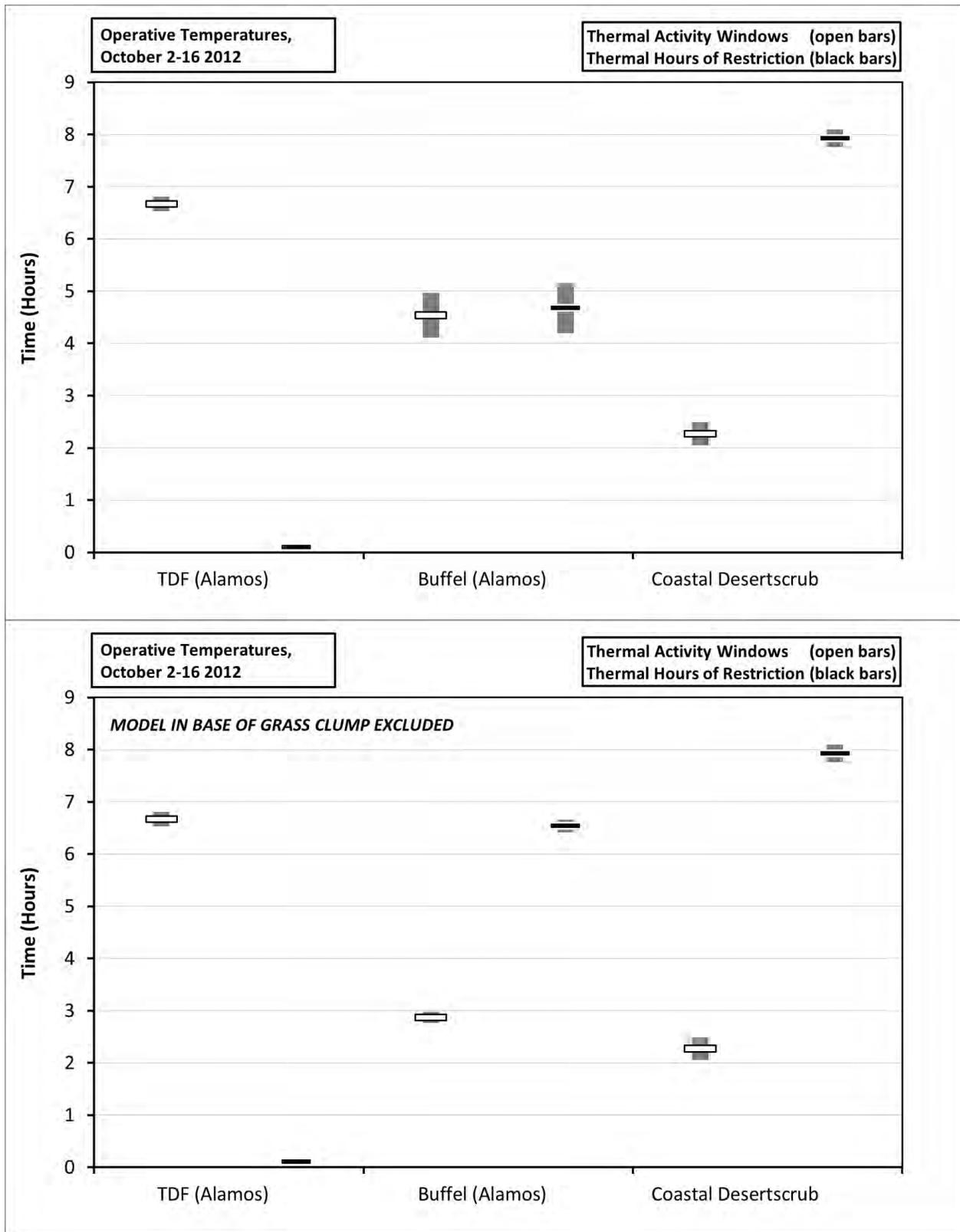


Figure 6.4. Thermal activity windows (h_a) and thermal restriction of activity (h_r) for *Gopherus morafkai* in three environments in Mexico during 2-16 October 2012.

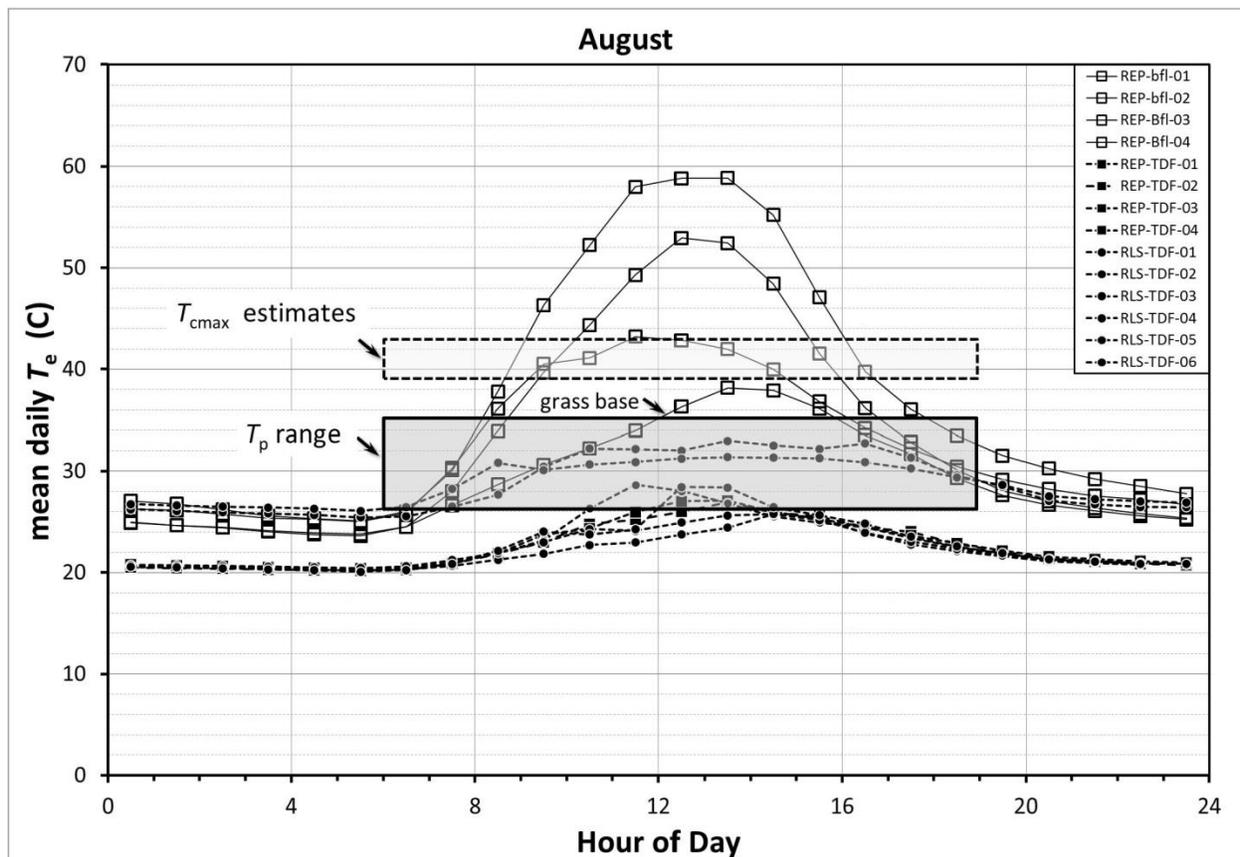


Figure 6.5. Hourly means of T_e for *Gopherus morafkai* measured in August 2013 in primary tropical deciduous forest (black symbols and dashed lines) and induced buffelgrass pasture (hollow symbols, solid lines) near Alamos, Sonora. Gray bars portray T_p (lower, darker; based on *G. agassizii* in Zimmerman et al. 1994) and critical thermal maximum measures (T_{cmax} ; above, lighter).

6.4 DISCUSSION

The operative thermal environment (T_e) of desert tortoises in tropical deciduous forest is strikingly different from that experienced by *Gopherus agassizii* in Mojave Desert (Zimmerman et al. 1994) or in the Sonoran Desert site we studied. In desertscrub, the incomplete plant canopy cover and the extent of open ground surface directly exposed to full insolation cause ground and air temperatures to soar not long after sunrise and to reach lethal T_e within one to a few hours in coastal Sonoran Desertscrub even in early October. Tortoises in desertscrub have narrow h_a windows in which to feed, perform social behaviors, and move within home ranges to locate optimal areas for foraging, sheltering, and breeding. A *G. morafkai* in desertscrub that is somehow prevented from accessing expected shelter and forced to remain aboveground as morning temperatures soar may display determined, if almost frantic search for a suitable shelter (T. Edwards, pers. comm.), and for good reason. Tortoises cannot really sprint for shelter, and they are so large that shelters are not always readily available. On very hot days, the suite of shelters available below lethal T_e may decrease: lethal exposure is a threat and could be a significant mechanism of mortality.

In contrast, TDF is so shaded in the summer rainy season that thermally determined h_a is lower during prime activity months (July-October) than in dry season when tortoise activity is much lower (March-

June). Yet throughout this period of months, tortoises in TDF have 5-7 hr/day thermally suitable for activity. In TDF, tortoises rarely encounter potentially lethal T_e , and essentially always have sub-lethal shade temperatures close at hand. Some portion of TDF habitat is frequently at T_e considerably below T_p —assuming *G. morafkai*, and specifically those populations of it with Sinaloan genotypes, are at least roughly similar in thermal physiology to *G. agassizii*.

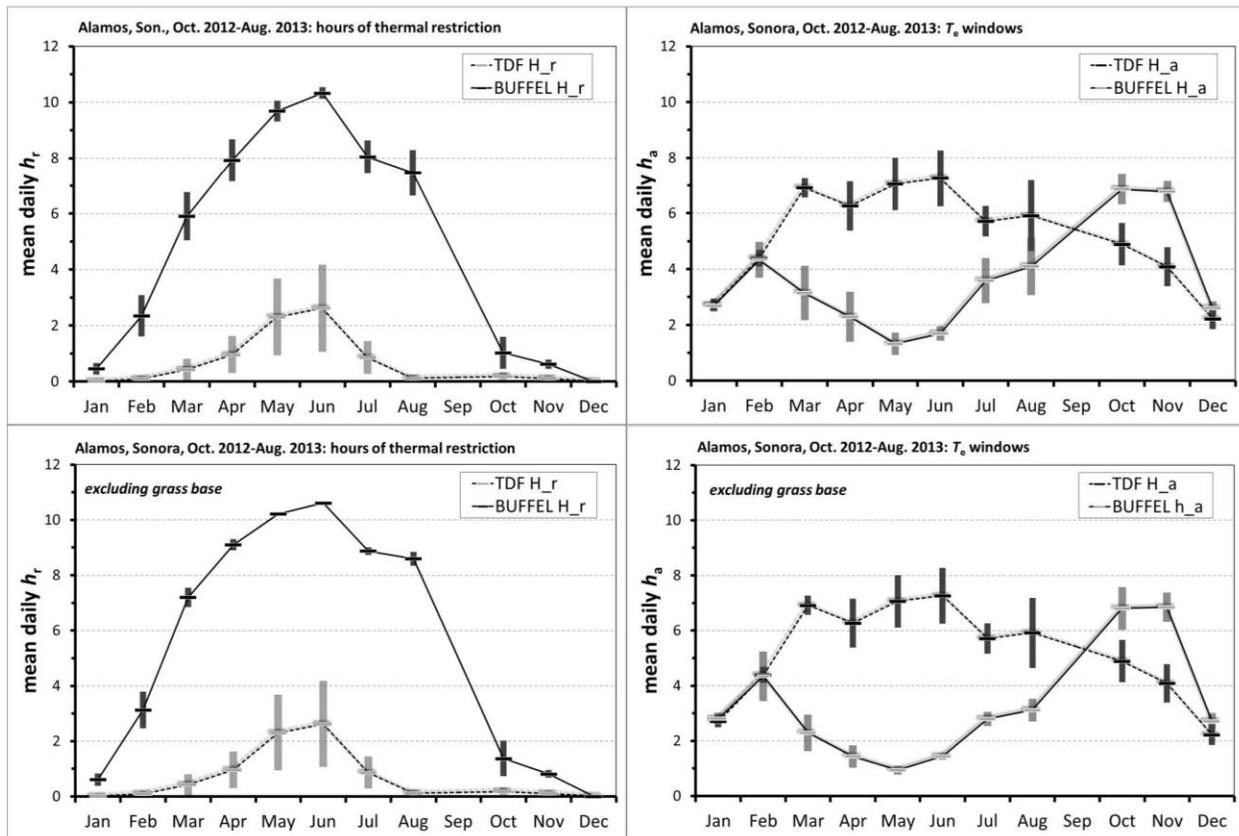


Figure 6.6. Annual profiles of h_r (left) and h_a (right) for *Gopherus morafkai* in primary tropical deciduous forest and induced buffelgrass pasture near Alamos, Sonora, October 2012-August 2013. Results were computed based on potential activity from sunrise to sunset. In the two lower graphics, data from a T_e model placed deep within a grass clump has been deleted.

Genetic divergence among Mojave, Sonoran, and Sinaloan lineages of desert tortoises is estimated to be about 5 million years old (Edwards et al. 2012, and *submitted*), which is sufficient for physiological divergence, at least in the absence of historical or genetic constraints on adaptation. The assumption used here that T_p in Sinaloan tortoises is similar to that in Mojave tortoises must be viewed as questionable unless verified by data. Not only do Sinaloan tortoises never face lethal temperatures in TDF, they frequently encounter an environment in which T_e below T_p is prevalent, even during the warm seasons. A significant part of the range of Sinaloan tortoises is in thornscrub, which is intermediate in shade availability between desertscrub and TDF, although mean annual air temperature in thornscrub occupied by the Sinaloan genotype are the highest of those experienced by any desert tortoises (Chapter 2). This might constrain physiological differentiation.

In the hot thornscrub occupied by Sinaloan tortoises and populations with mixed Sinaloan-Sonoran genetics (Edwards et al. 2012, and *submitted*), we found high proportions of carcasses in field samples (Chapter 2). In other parts of the (currently recognized) range of *G. morafkai*, high mortality was consistently associated with drought and population declines; although drought and high temperatures are correlated, drought was a stronger predictor of mortality (Chapters 2-5). Mortality in low elevation thornscrub was discovered each time we sampled there during 2006-2013, but we lack temporal resolution to determine correlations of mortality with drought versus high temperatures. At the lowest elevations, Sinaloan Thornscrub is difficult to distinguish from less arid parts of the Sonoran Desert (this biotic community was classified as Foothills of Sonora province of the Sonoran Desert [Shreve 1951] until its more tropical character, and relatively greater rainfall, was highlighted by Felger and Lowe [1976]). In some of the arid thornscrub sites at lower elevations where mortality was found, average rainfall may be well over twice that at corresponding elevations occupied by tortoises in Sonoran Desert (Chapter 2): drought is therefore expected to be less frequent, and direct effects of rising temperatures via h_r or lethal overheating may be more likely than in other environments, which are all generally less hot.

Two striking aspects of T_e in induced buffelgrass pasture are (1) the apparently ameliorated thermal regime in buffel compared to desertscrub, which is a preliminary finding based on only 12 days of monitoring, and (2) the marked deterioration of thermal regime in buffel compared to TDF. Our data suggest that induced pasture in desertscrub, in which trees are allowed to persist as now legally required, may have some benefit to tortoise thermal physiology in addition to known negative effects via fire and dietary impacts (see Chapter 1). However, in TDF, induced pasture appears to produce a huge deterioration of habitat quality for tortoises. In some Sinaloan Thornscrub sites we studied there were large areas of induced pasture, savannah-like in structure, and tortoises would likely be highly vulnerable to lethal temperatures and h_r effects in these habitat areas. Although thornscrub has been targeted in Sonora for conversion to induced buffelgrass pasture (Búrquez et al. 2002), buffelgrass was not a major component of the pastures we surveyed (in the Suaqui Grande region). However, T_e in induced pasture in thornscrub is highly likely to be detrimental to tortoises with or without buffel dominance, as most other grasses have less thermal buffering of the ground surface than buffel.

Our results suggest that induced pasture in thornscrub is likely to have adverse effects on *G. morafkai* populations, and is virtually certain to do so in tropical deciduous forest. The forest rapidly reclaims buffelgrass pastures that are not actively maintained by slashing and burning, and there is some evidence for this in thornscrub as well (Chapter 1). Active management to restore habitat quality for desert tortoises in these two environments may be achieved as easily as releasing successional forces. If Mexico's trajectory of modernization and economic improvement continues, the currently positive attitude toward biodiversity in the country is likely to tip the balance between pasture and native biota in the tortoise's favor, particularly if the threats to biodiversity are well known.

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Chapter 7 Ecological Observations on Desert Tortoises in Mexico

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ABSTRACT

We sampled *Gopherus morafkai*, Morafka's, or Sonoran Desert tortoise) across its geographic distribution at 43 localities, at 37 of which we found tortoises, in northwestern Mexico during 2005-2013. Observed relative abundance did not differ among desertscrub, thornscrub, and tropical deciduous forest, although sampling was more difficult in tropical deciduous forest and we suspect that tortoise abundances are highest there, at least based on work in the Alamos region. Based on growth rings, desert tortoises we observed in desertscrub averaged older than those in thornscrub and tropical deciduous forest, with the difference occurring in pre-adult age classes. These data suggest that desert tortoises in tropical deciduous forest, and possibly in thornscrub, grow more rapidly to adult size than those in desertscrub.

7.1 INTRODUCTION

In this chapter we present preliminary data and analysis on abundance, age structure, and growth for desert tortoises in northwestern Mexico. More detailed analysis is in progress.

7.2 METHODS

7.2.1 Transect Surveys During 2012-2013

We used transects recorded by handheld Garmin™ GPS units (accuracy 3-4 m) to record and archive location- and time-specific quantified data on encounter rates of tortoises, other herpetofauna, as well as predators. Each fieldworker carried a GPS unit, digital camera, and gear needed to measure and weigh tortoises using established protocols to avoid disease transmission. Each person searched independently for tortoises, recording a track (time and location) with waypoints for each tortoise observation. Experienced observers also recorded waypoints for each amphibian or reptile observed on the transects. A coding system was used for waypoints and notations in a notes field in the GPS units, to provide necessary details such as species, sex, size, age-class, measurements, microhabitat, and reference to other notes maintained in writing.

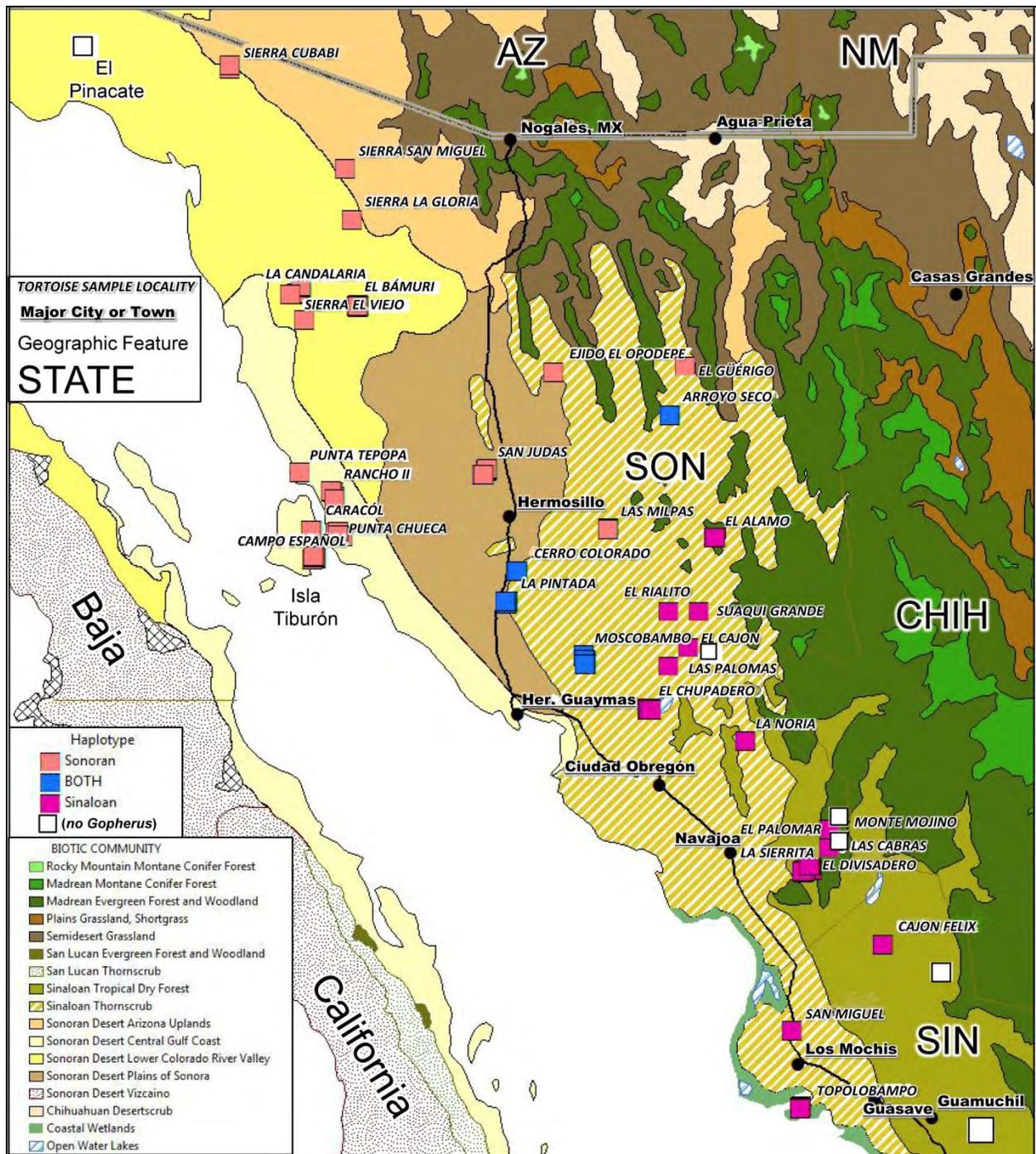


Figure 7.1. Sampling locations, 2005-2013. In 2012-13 we sampled at (from north to south) Sierra El Viejo, Rancho El Bámuri, Rancho El Güérigo, Rancho Arroyo Seco, Rancho El Alamo, Punta Chueca, El Rialito, Suaqui Grande, Rancho El Cajon, Rancho Las Palomas, Moscobampo, Reserva Monte Mojino (including ranchos El Guayabo, El Palarito, and nearby La Majarra; and at La Chalate and Rancho Santa Barbara, where we found no tortoises), Rancho El Palomar, Rancho La Sierrita, Rancho El Divisadero, and two localities in Sinaloa at which we found no tortoises.

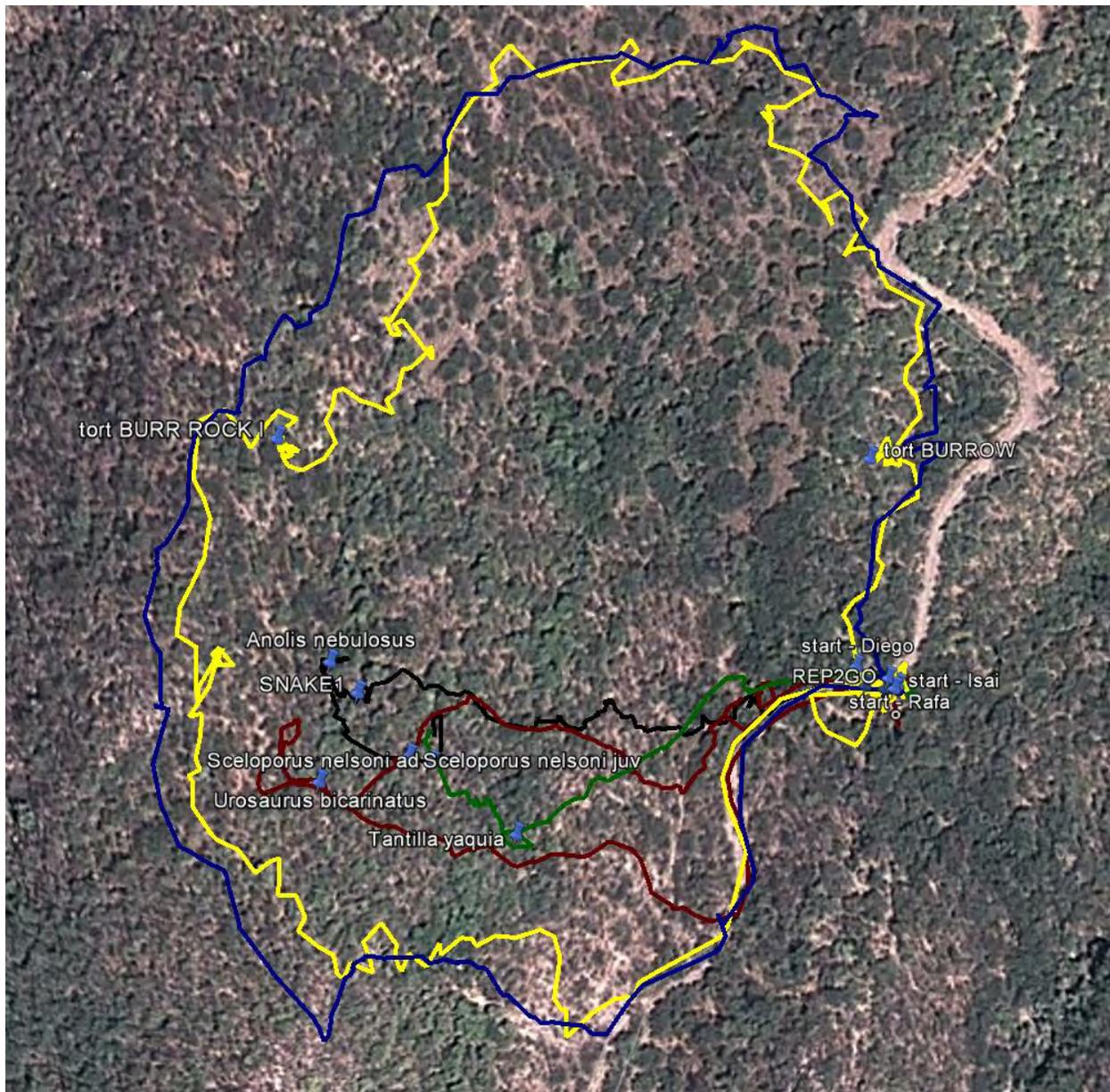


Figure 7.2. Example of a single set of transect tracks and waypoints in TDF, Rancho El Palomar, Alamos, Sonora, 29 September 2012, projected onto a Google Earth image of the landscape.

Waypoints were similarly recorded for each observation of tortoises and their sign. Data for each live tortoise was written on a paper data sheet, and included sex, growth ring count, injuries, signs of illness, shell measurements, body mass, activity, behavior, microhabitat and, where applicable, burrow characteristic, photographs taken, waypoint names, and observer. Tortoise burrows, scat, tracks, and other potential unknown observations (such as unidentified species of amphibians and reptiles) were photographed. Tracks, waypoints, and photographs were maintained in digital folders under the names of the observers, and subsequently waypoints were transferred a spreadsheet file with associated information translated to a standardized data format. GPS tracks were processed in Garmin Mapsource™ to eliminate extraneous legs attached to the tracks and to remove time and movement not part of

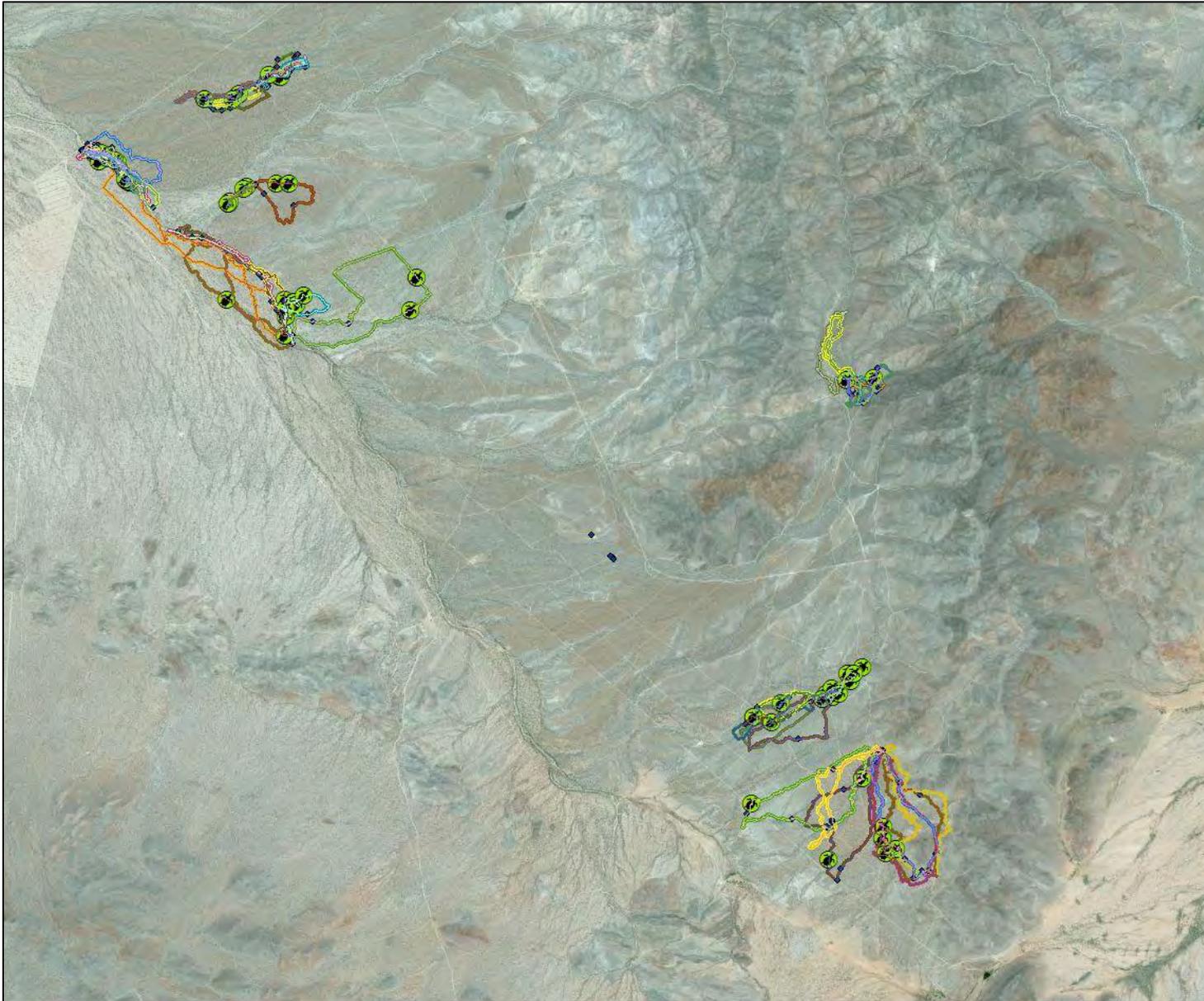


Figure 7.3. An overview of transects and locations of tortoises and tortoises sign other herpetofauna at Rancho El Plomito, Sierra El Viejo, Caborca, Sonora, 9-11 October 2012, projected onto aerial imagery in ArcGIS. Green symbols are tortoise records.

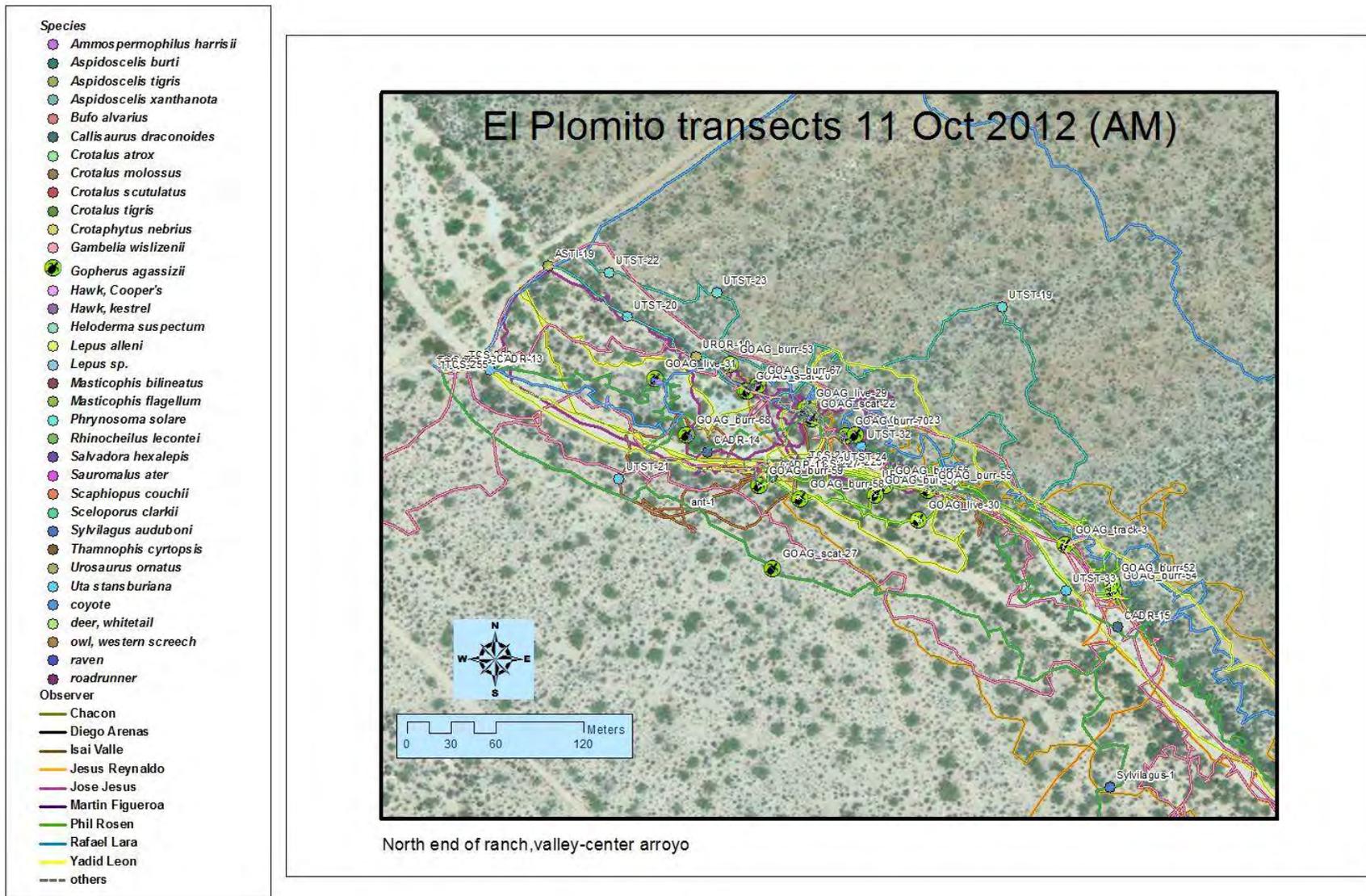


Figure 7.4. Example of transect results in displayed in ArcGIS.

the transects (such as waiting at the start and end points of the transect). Each track then contained a record of the total time and distance covered by one observer on one transect (see Figs. 7.2-7.4).

7.2.2 Use of Growth Rings

Use of growth rings on chelonian shells have been controversial (Bury, and others), understandably for tropical turtles in relatively aseasonal climates (Moll and Legler 1971), but specifically for desert tortoises (summarized by Ernst and Lovich (2009). Berry (2002) reported that photographs of annuli increased, on average, by close to one per year, but this varied dramatically among regions, while Germano (1998) suggested that growth rings were accurate if counted by experienced workers, although he offered no conclusive support for this. In Sonoran Desert, tortoises live under greater rainfall than in Mojave Desert, where this argument has been focused, and it is less likely that tortoises would skip a growth year entirely, as summer rains are relatively reliable in Sonoran Desert and the variability of precipitation rises steeply as total precipitation declines in desert climates (Warner 2004). We have no indication that desert tortoises in Sonoran Desert produce a spring and then a similar summer growth ring, and although this has not been addressed we should have reports of gross inconsistencies between growth rings and age estimates, which we do not. The appearance of growth rings we report here suggests that they are consistent and annual, but we nonetheless cannot verify this and thus report them provisionally.

In 2012-2013, we photographed all tortoises dorsally, laterally, ventrally, and frontally. We photographed shell annuli on all tortoises we handled using high-resolution digital cameras (2816 X 2112 pixels), using two images: one image portrayed the entire 1st lateral (or costal) scute and a second close in to the lower portion of the same scute showing the smaller annuli from later, slower growth and permitting an accurate determination of which scute they were on (lateral or marginal) (Figs. 7.5 and 7.6). One of us (Rosen) examined these photographs on screen and counted all complete rings that appeared to be roughly similar in depth, ignoring any apparently shallow annuli, which are present on all turtles, that were assumed to represent temporary growth stoppages or reductions. There was little ambiguity except for the oldest annuli (from the first 1-5 years of life), which are also often the most worn. The oldest annuli were all counted if visible, because growth is known to be slow at very young ages based on the literature (Ernst and Lovich 2009) and observations of annuli on the smallest desert tortoises, both wild ones and those in captivity of known ages. The most definite counts were from individuals on which the slightly textured birth plate was visible, and we enhanced the number of these cases by examining the 4th lateral, which is relatively protected from scraping when the tortoise moves forward and better retains the annulus record of early life. This scute was usually visible on dorsal and lateral photographs, but we also took supplemental images of this scute when aging, which done in a preliminary fashion in the field, appeared difficult. When the earliest annuli were not visible, the number missing was recorded as a range of possible values based on other records in our sample. A single number is presented here as the mean of the extremes of these estimates or the most likely age assigned during the inspection of digital images. Thus an age recorded as "24-27 (26)" is here reported as 26.



Figure 7.5. Growth rings (annuli) of a Sonoran Desert tortoise (upper left) and Tropical Deciduous Forest tortoise (upper right). Lower images show 4th costal (lower left) and 1st costal (lower right from the same tortoise, illustrating reduced wear on the former).



Figure 7.6. Close-ups of recent annuli on a TDF tortoise (top) and Sonoran Desert tortoise (bottom).

7.3 RESULTS

7.3.1 Habitat

We found desert tortoises in almost all areas we searched that included at least some substantial rock formations (bedrock, boulders, and cemented alluvium such as caliche and conglomerate rock) within \leq \approx 1 km (Fig. 7.7). Certain rock types have no shelter sites for tortoises in local areas that may include entire canyons; nonetheless, even sites with minimal rock shelters yielded tortoise sign, at least in the form of scat or carcasses. However, we studied two notable habitat areas with sizable desert tortoise populations in which rock formations were scarce and were a minor part of the utilized environment. We provide some brief details here.

At Sierra El Viejo and Rancho El Bámuri, in Lower Colorado River Valley Sonoran Desertscrub southwest and south of Caborca, respectively, we conducted numerous transects in varied habitats in 2012-13, including a systematic sampling of Rancho El Plomito in the southwest quadrant of Sierra El Viejo. Habitat types we surveyed (Figs. 7.8 and 7.9) included (1) several canyons with thin soils overlying extensive limestone bedrock, one of which also contained extensive rims of collapsing and eroding conglomerate rock with, (2) bajada arroyos, all with extensive outcrops of conglomerate and caliche, (3) bajada uplands with variable, mostly thin soils, and a major, mid-valley braided arroyo with a rich xeroriparian bosque but no bedrock and little caliche or conglomerate rock and few rock-based shelter sites. Although we found no live tortoises in the six canyons we surveyed, there was a small amount of scat present in one, and dead tortoises were found in the mouth of two others. Bajada arroyos that we surveyed all yielded extensive tortoise sign and including scat, tracks, active burrows, and in all but a single case, live tortoises. Tortoises were also found in abundance during morning and late afternoon activity periods on bajada uplands near (within \approx 400 m) bajada washes, and burrows were found where soils were deep. The most striking feature of this study region was the presence of a dense population of tortoises in the mid-valley arroyo (Figs. 7.4 and 7.9). Throughout this region we found extensive use of soil burrows by tortoises, although we only made observations during August-October and have no information on seasonal variation in burrow type use.

In Tropical Deciduous Forest on Rancho El Palomar at the north margin of the town of Alamos, we found numerous tortoises in extensive sampling in rolling hills intermixed with pastures in low-lying environment (Fig. 7.10). Although there were rock walls separating pastures and widely scattered boulders, most tortoises were found surface active or associated with soil burrows or surface cover. In October, we found tortoises active in buffelgrass and other non-woody vegetation in the pastures. We also found tortoises in the higher, more rocky and mountainous portion of the ranch, including small juveniles, as well as spotted box turtles (*Terrapene nelsoni*) and painted wood turtles (*Rhinoclemmys pulcherrima*). Although we were unable to find intact TDF in low-lying environments to sample in the Alamos region, our results at El Palomar indicate clearly that tortoises in the TDF are not confined to or primarily found in rocky, mountainous terrain.



Figure 7.7. Examples of rocky environments utilized by desert tortoises in Mexico (upper left – TDF at Rancho El Palomar; upper right – TDF at Rancho La Sierrita; lower left – freeze-killed thornscrub at Rancho El Güérigo; lower right – limestone formations unsuitable for tortoises at Sierra El Viejo).



Figure 7.8. Bajada habitat at Rancho El Plomito, Sierra El Viejo, in Sonoran Desertscrub southwest of Caborca. Major bajada arroyos (top left) had extensive outcrops of conglomerate and caliche rock forming shelters, and smaller such arroyos also supported such habitat (upper right). Thin bajada soils were mostly unsuitable for burrowing, but not entirely (lower left, active burrow at center). An active burrow from the upper right scene is shown at lower right.



Figure 7.9. Habitat of a high-density tortoise population in mid-valley bottomland west of Sierra El Viejo, Rancho El Plomito. Some of the numerous soil burrows near or in which tortoises were found are shown at lower right and lower left.



Figure 7.10. Tortoise habitat among rolling hills and low mountains in TDF and pastures (upper left) at Rancho El Palomar. Tortoise were found in or near brush piles (upper right, with tortoise shown in inset), soil burrows (lower left) and in widely scattered boulder (lower right) and rock wall microhabitat.

7.3.2 Relative Abundance

Observation rates of live tortoises and tortoise burrows did not differ among the three biotic communities we sampled (Fig. 7.11; Tables 7.1 and 7.2). There were no significant differences among biomes in encounter rates for live tortoises, burrows, or total sign (excluding dead tortoises) on standardized GPS transects. Significantly more sign records for scat and tortoise tracks were found in desertscrub, very likely due to the much higher visibility and surfaces that recorded tracks, compared to the thornscrub and tropical deciduous forest (Table 1).

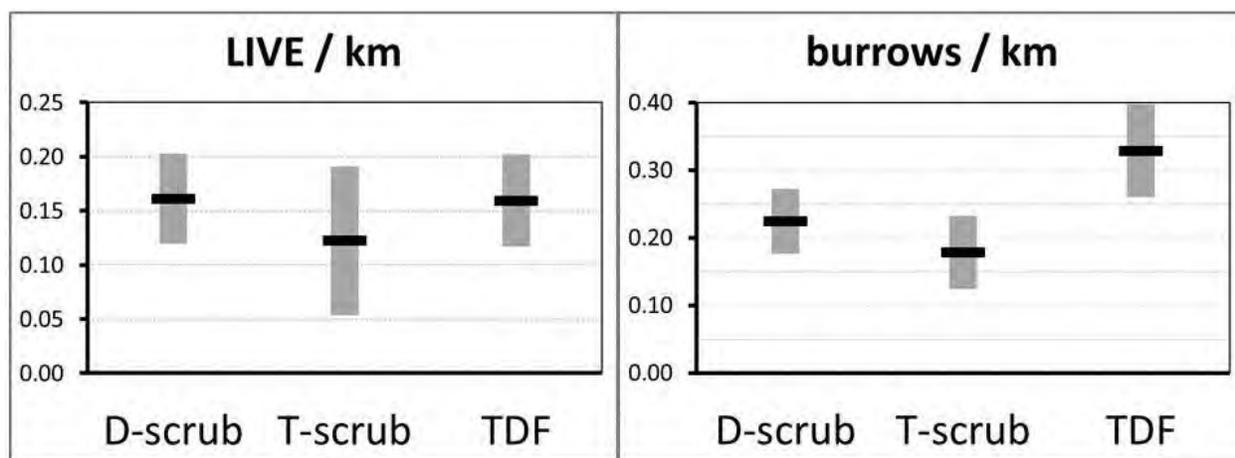


Figure 7.11. Observation rates of live tortoises and tortoise burrows on *G. morafkai* transects in northwestern Mexico, 2012-2013.

Table 7.1. Transect totals for *G. morafkai* in northwestern Mexico, 2012-2013.

Transects (2012-13)			Desert Tortoise Sign Records				
Biotic Community	Transect Sets (N)	Transect km (Total)	LIVE	DEAD	burrow	scat	track
Desertscrub	22	389.1	47	6	79	35	13
Thornscrub	12	137.8	11	5	23	3	
TDF	31	244.3	27	1	48		
Overall	65	771.3	85	12	150	38	13

Table 7.2. Encounter rates of live tortoises and burrows on transects in northwestern Mexico, 2012-2013, at localities in which tortoise presence was detected, including by all forms of sign.

Biotic Community	LIVE / km	SE LIVE	burrows / km	SE burrows
Desertscrub	0.161	0.042	0.225	0.048
Thornscrub	0.122	0.069	0.179	0.054
TDF	0.159	0.043	0.329	0.069
ALL	0.153	0.027	0.259	0.035

7.3.3 Age Structure, Growth Curves, and Size Inferred from Growth Rings

Based on growth rings interpreted as annular rings, age structure differed significantly among biomes (Figs. 7.12 and 7.13; Table 7.3). There were higher proportions of tortoises of younger ages in TDF and thornscrub than in desertscrub, with strongly significant differences between desertscrub and marginal differences between desertscrub and TDF. However, for presumptively adult-sized tortoises (MCL \geq 210 mm), desertscrub and TDF tortoises were similar in size (Fig. 7.12), with nearly equal median values (24 and 24.5 years, respectively) and means for adults with 20 or more annuli (25.9 versus 25.8 years, respectively).

Table 7.3. Comparison of age structure of *Gopherus morafkai* from different biomes in Mexico for the transect-based study in 2012-13 and for 2005-2013 overall.

Biome	Estimated Age (Annuli)			Tukey-Kramer grouping	pairwise- <i>t</i> grouping
	N	Mean	SE		
<u>2012-2013 transect study</u>					
Desertscrub	62	23.29	0.90	A	A
Thornscrub	18	17.72	1.66	B	B
TDF	30	18.57	1.29	B	B
<u>2005-2013 overall</u>					
Desertscrub	89	22.57	0.74	A	A
Thornscrub	22	17.36	1.49	B	B
TDF	61	20.18	0.89	AB	B

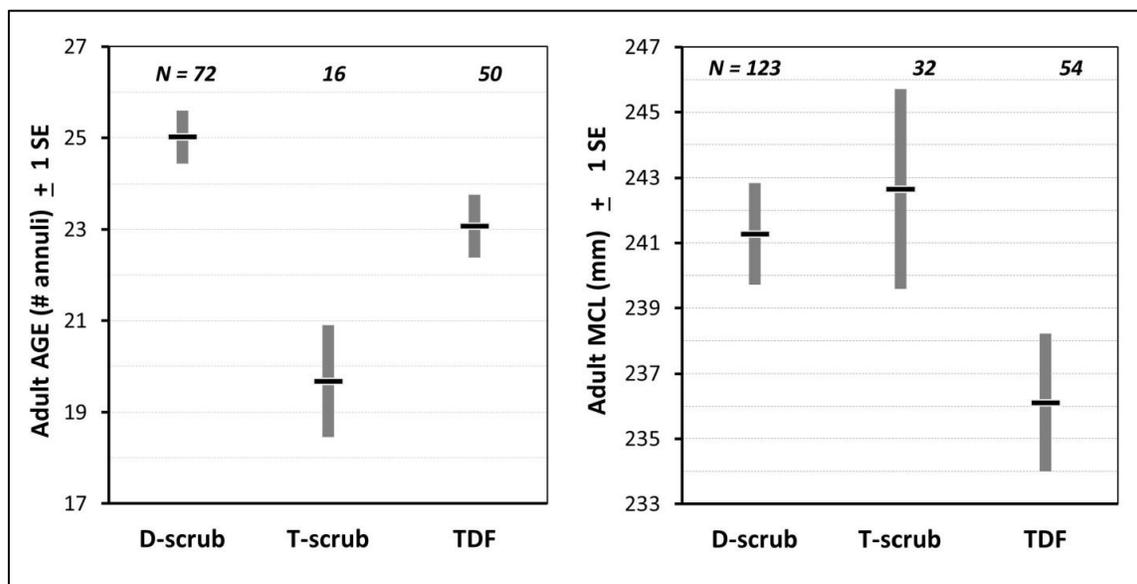


Figure 7.12. Comparison of carapace length (MCL) and estimate age (based on annuli) of *Gopherus morafkai* for three biomes in Mexico, 2005-2013.

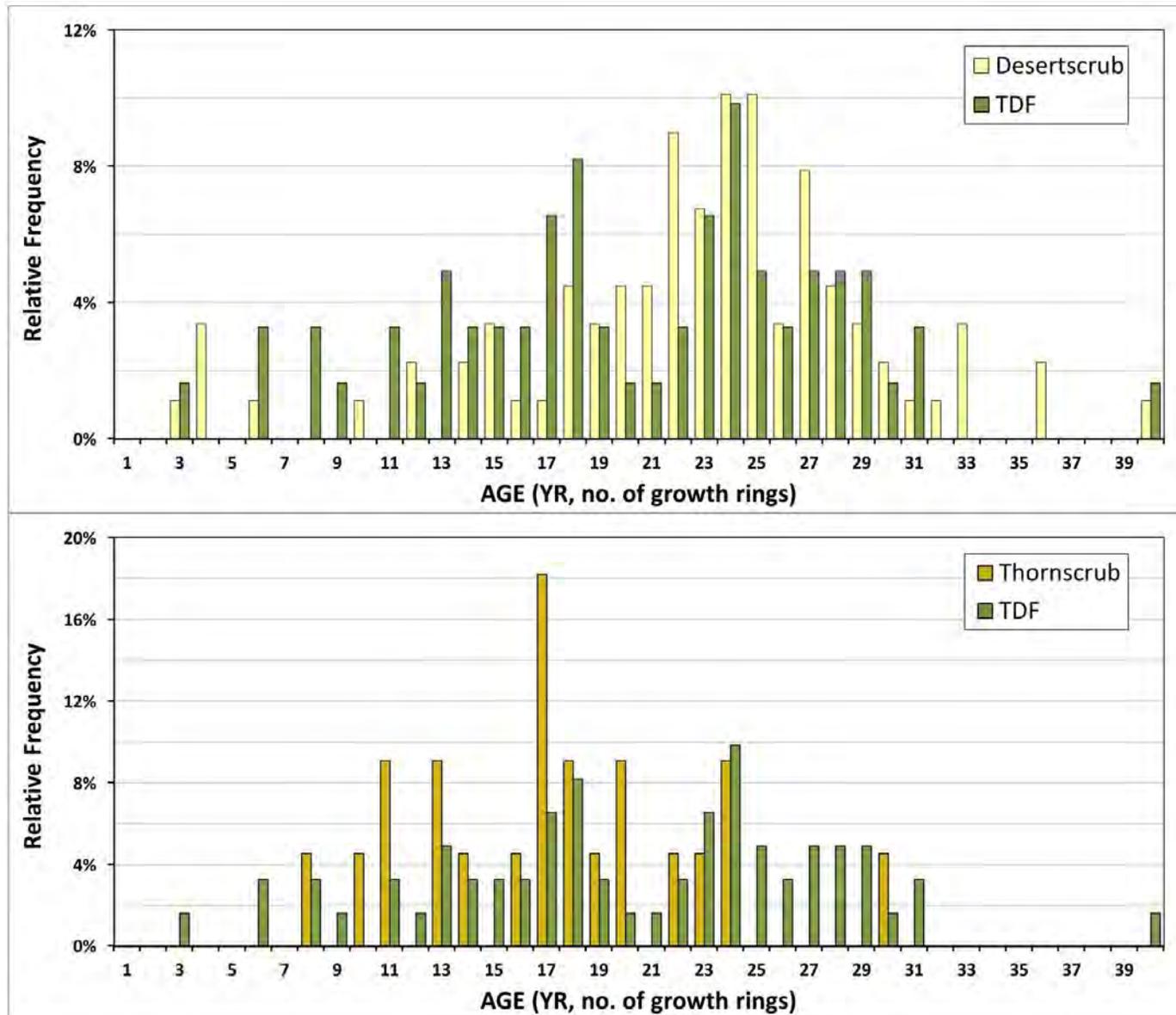


Figure 7.13. Age structure inferred from growth rings of desert tortoises in northwestern Mexico, 2005-2013.

Mean size of adults was smallest in TDF and similar in desertscrub and thornscrub (Fig. 7.13; $t = 2.16$, $P \approx 0.03$ for TDF versus desertscrub). Based on annuli, desert tortoises in Mexico grew faster toward presumptive adult size in thornscrub and TDF than in desertscrub (Fig. 7.14). Modeling growth by curve-fitting using the Richardson growth equation (Fig. 7.14, Table 7.4) proved difficult for TDF especially, as we were unable to fit a curve that captured the marked transition from rapid juvenile growth to relatively very slow adult growth. However, the modeling results consistently produced smaller asymptotic body size for TDF (MCL = 272 mm) than for desertscrub (MCL = 294 mm). The sample size of

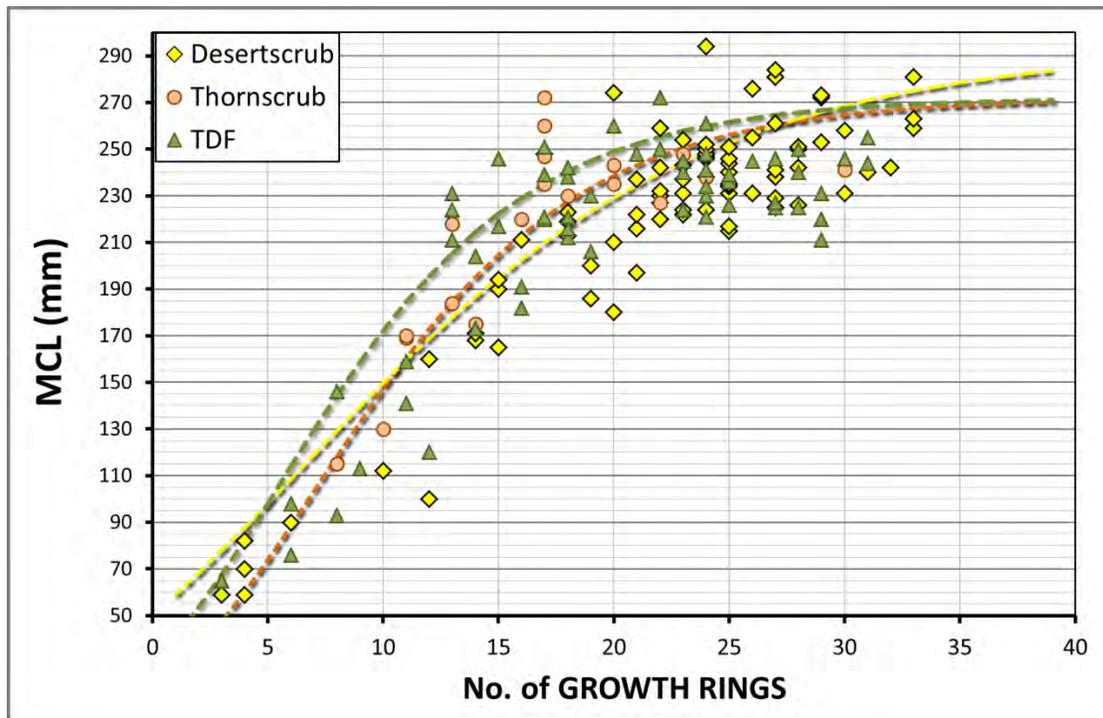


Figure 7.14. Size, age (number of annuli), and computed growth curves for desert tortoises in three biomes in northwestern Mexico based on all individuals 2005-2013 with available photographs suitable for counting annuli.

Table 7.4. Richardson equation growth-curve modeling parameters for *Gopherus morafkai* in Mexico. Parameters we fixed are indicated as "input".

Parameters	Desertscrub	Thornscrub	TDF
A (asymptotic size)	294	272	272
μ (growth rate parameter)	10.48	14.99	15.85
λ (lag-phase parameter)	-4.341	0.092	-1.188
hatchling size (mm, age = 1; input)	46	46	46
ν (shape parameter, input)	0.1	0.1	0.01

age estimates for thornscrub was too low for accurate modeling, and although the growth curve is shown for completeness in Fig. 7.14, it indicates a value for asymptotic size (MCL = 272 mm) that may be too low based on Fig. 7.13. The difficulty fitting the growth model resulted in asymptotic sizes equal to

the largest tortoises we found in desertscrub (MCL = 292 mm) and TDF (MCL = 272 mm), but smaller than the largest size we found in thornscrub (MCL = 282).

7.4 DISCUSSION

We suspect that desert tortoises in Mexico are more abundant in TDF than in desertscrub or thornscrub for three reasons. First, visibility is lowest and transect sampling most difficult in TDF; second, we sampled more previously unknown localities in TDF than in desertscrub or thornscrub in 2012-2013, which added data from localities that may have been less optimal; and third, we specifically sampled one site of special interest in Sonoran Desertscrub, Sierra El Viejo, intensively in both 2012 and 2013, which yielded unusually high rates of observation in desertscrub. Fritts and Jennings (1994) also believed tortoises were more abundant in TDF than in other habitats in Mexico.

We suspect that age structure differs among the three biomes, although the general lack of smaller animals in all biomes is undoubtedly partly because small animals are difficult to find. To explore growth and age at maturity, we would need to verify the age determinations based on growth rings, as well as increase sample size in thornscrub, and increase sample sizes for older animals in thornscrub and TDF.

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